

STUDIES IN NEOTROPICAL PALEOBOTANY.
II. THE MIOCENE COMMUNITIES
OF VERACRUZ, MEXICO^{1, 2}

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ABSTRACT

Lignites containing a diverse and well-preserved pollen and spore flora were obtained from the upper Miocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico. Among modern communities reflected in the fossil microflora are Needle-Leaved Forests of bosque de oyamel, bosque de pino, and bosque de pino y encino; Broad-Leaved Forests of warm, temperate and evergreen oak communities; Deciduous Forest; Temperate and Saline Grasslands; Mangrove Swamps; Coastal Dune Vegetation; a restricted and modified Low Deciduous Selva; and possibly Paramo, Inland Swamp, and Aquatic Vegetation. Absent or poorly represented are the Scale-Leaved Forests of bosque de cedro y táscate; High Evergreen Selva (tropical rain forest); High Semi-Evergreen Selva; Medium Semi-Evergreen Selva; Low Evergreen Selva; Low Semi-Evergreen Selva; Low Thorn Selva; Palm Stands; Savannas; *Nolina*-

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² These investigations on the Cenozoic history of Mexican vegetation began in 1965, and during the period of study many individuals have provided assistance that is greatly appreciated. Dr. J. Rzedowski, Instituto Politécnico, made arrangements through Dr. Cortez Obregon for cooperation of the Consejo de Recursos Naturales No Renovables. Dr. Cortez Obregon supplied coal and lignite samples from several localities in Mexico, and Dr. Rzedowski has continued to provide very helpful information on Mexican vegetation.

In 1967 Dr. Arturo Gómez-Pompa arranged discussions with Dr. Agustín Ayala-Castañares and Ing. Guillermo P. Salas, Instituto Geología, UNAM, concerning various facets of Mexican geology. As a result of these discussions, samples were eventually obtained from Coatzacoalcos, Veracruz through the offices of the Petróleos Mexicanos and Ing. Roberto Gutierrez Gil, Superintendente, Zona Sur. Subsequently other geological information was provided by Dr. Jaime Rueda-Gaxiola, Instituto Mexicano del Petróleo. During the 1967 field season Dr. David Jarzen and Dr. Enrique Martínez-Hernández capably assisted in the collection of samples.

Interpretation of the palynological data has been facilitated by numerous conversations with members of the Departamento de Botánica, UNAM, including Drs. Ramon Riba, José Sarukhán, Mario Sousa, and Dr. Arturo Gómez-Pompa. In addition to providing valuable suggestions on the distribution and ecological significance of taxa identified from the Paraje Solo microflora, Dr. Gómez-Pompa organized a visit to Veracruz in 1971 for study of various community types represented in the fossil assemblage.

Of particular importance to this study are data and publications resulting from the Flora Veracruz Project (see Gómez-Pompa & Nevling, 1970). As a guide for processing relevant pollen and spore reference material and for distribution information, it is necessary to know the composition of the regional vegetation. In previous studies on Latin American paleobotany accumulating this information from herbarium sheets has been a lengthy and tedious task. As part of the Flora Veracruz Project a computer program has been designed, and this facet of the project has been of inestimable value for our studies on the vegetational history of Veracruz. Rather than the 2-3 months required to accumulate a list of important plants in the modern flora, a print-out of 6,049 species names was generated in less than 30 minutes. The completion of the Flora Veracruz will be an important contribution to the botany of Latin America, and in the meantime general summaries of the vegetation and soils (Gómez-Pompa, 1973), climates (García, 1970), and the developing retrieval system are most appreciated by those of us dependent on information about the modern communities.

A number of individuals provided helpful information on specific points of the study, including especially Drs. Dennis Breedlove, Michael D. Coe, Paul Colinvaux, Margaret Davis, E. S. Deevey, Richard A. Howard, Daniel Livingstone, Rogers McVaugh, Lorin Nevling, Reinhard Weber, and H. E. Wright.

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Hechtia-Agave Desert; and Thorn Scrub. The presence of pollen of *Picea* in the microflora suggests cooler temperatures during the upper Miocene and possibly greater and more uniformly distributed rainfall. This type of paleoenvironment would account for the poor representation of both the tropical rain forest and communities of arid aspect, and account for the prominence of the temperate Deciduous Forest in the upper Miocene paleocommunities.

The region of southern Veracruz is biologically one of the most interesting in northern Latin America. Because of its location at a transition between tropical and temperate environments, with topographic diversity ranging from sea level to the highest altitudes in Mexico, an array of vegetation types and considerable species diversity characterizes the flora. The lowlands contain remnants of a tropical rain forest (*Selva Alta Perennifolia*) with floristic affinities primarily to the south, while the mid-altitude eastern slopes of the Sierra Madre Oriental support an oak-*Liquidambar* deciduous forest (*Bosque Caducifolio*) containing some 60 species of arborescent plants also found in the temperate forests of the eastern United States. Historical factors have been important in the development of the biota since southeastern Veracruz is situated at the confluence of an Antillean-Central American migration route that has operated throughout the Cenozoic. With land surfaces gradually increasing in the Greater and Lesser Antilles during the Tertiary, and climatic fluctuations affecting the range of various neotropical species, numerous floral and faunal elements have converged on and radiated from the intersection of these two migration routes. The diversity in habitats, available since the initial uplift of the Sierra Madre Oriental beginning near the end of the Cretaceous, and continuing through the Cenozoic, allowed many of these elements to persist, creating a diverse flora estimated at some 10,000 species.

The region is also of interest as the site of one of the oldest sedentary agricultural populations in Latin America. The "Olmec Heartland" was being occupied and cultivated nearly 5,000 years ago, near the end of the climatic Xerothermic Period (ca. 8,000–4,000 B.P.), and several plant associations present today, but absent or poorly represented in the Miocene flora, may be attributable to the milpa farming practices of the Olmecs and subsequent civilizations introduced near the end of a prolonged dry period (e.g., savannas, palm stands of *Scheelea* and *Sabal*, and certain communities of dry aspect).

The Veracruz studies were undertaken to provide a better understanding of the vegetation and its development during the Cenozoic. The preliminary results indicate, however, that rather than confirming earlier impressions, considerable revision is necessary in our concepts of the vegetation of the region. For example, the existing literature suggests that elements of the deciduous forest (*Acer*, *Juglans*, *Fagus*, *Liquidambar*, *Alnus*, *Ulmus*, *Populus*, *Platanus*, *Cornus*, *Salix*, and others) are recent introductions corresponding to times of maximum glacial advance, while the tropical rain forest is an ancient community occupying lowland regions of stable unchanging environments. In fact, elements of the temperate deciduous forest were already well established in southeastern Mexico by the end of the Miocene, and evidence is accumulating that the modern tropical rain forest may be of Post-glacial origin of less than 11,000 years.

In evaluating the Veracruz data it should be noted that there are no other Miocene microfloras published for Latin America, and the only megafossil flora is that discussed by Berry (1923). Virtually nothing is known of pollen release and transport or pollination mechanisms for important neotropical genera represented by pollen in the fossil assemblage, and only recently has the present-day vegetation been adequately enough characterized (Gómez-Pompa, 1973) to allow comparison of the modern and Miocene communities. These difficulties impart a tentative aspect to interpretations that undoubtedly will be altered and refined in future studies. For the moment, however, the near absence of information on vegetational history for northern Latin America warrants presenting even these preliminary data on the upper Miocene flora of southeastern Veracruz.

PHYSIOGRAPHY AND CLIMATE

Veracruz is the most physiographically diverse state of Mexico, extending through 5° latitude (17°10' to 22°20'N; Fig. 1). The state is mostly flat, low-lying coastal plain of less than 300 m elevation. In west-central Veracruz, however, two important mountain systems converge, a branch of the Sierra Madre Oriental and an eastern extension of the Cinturon Neovolcánico (Transvolcanic Belt). These mountains include the highest peak in Mexico, Pico de Orizaba (5,747 m). The major period of uplift began during the Cretaceous as part of the "Laramide Revolution" that characterized the end of the Mesozoic Era. These highlands are located about 325 km NW of the collection localities at Coatzacoalcos.

Another mountainous area in Veracruz is the Sierra de los Tuxtlas to the south and inland from the coast, about 100 km NW of Coatzacoalcos. These mountains are of volcanic origin and the exposed basalts are of Miocene-Pliocene age (Salas, 1968). The highest elevation is about 1,700 m. Climates of the northernmost portion of the state are influenced by the Sierra de Tamaulipas, around the port of Veracruz by the Sierra de Chiconquiaco, and in the southernmost part of the state by branches of the Sierra Madre del Sur which reach about 1,000 m. The Sierra de Tantima consists of a few low mountains about 700 m in elevation near Tantoyuca (see Fig. 1 for place names).

As a consequence of its longitudinal extent and topographic diversity the range of climates in Veracruz is extensive (García, 1970). Near the summit of Pico de Orizaba average annual temperatures are below -2°C and frost occurs about 40 days per year. At intermediate elevations along the east and west slopes of the mountains, at elevations between about 500 and 2,000 m, extending (N-S) from Chicontepec through Papantla, Jalapa, Córdoba, to Tierra Blanca, is a temperate zone with average annual temperatures between 12 and 18°C. The greatest portion of Veracruz (the coastal plain below about 300 m elevation) is hot with average annual temperatures between 22 and 26°C. In the vicinity of Veracruz and in low-lying inland areas and valleys to the south annual temperatures average slightly above 26°C.

Rainfall in Veracruz is from about 500 mm annually to more than 4,000 mm. Regions of highest rainfall are in the south, along the coast in the vicinity of San Andrés de Tuxtla (ca. 4,000 mm) and along the western border of the state

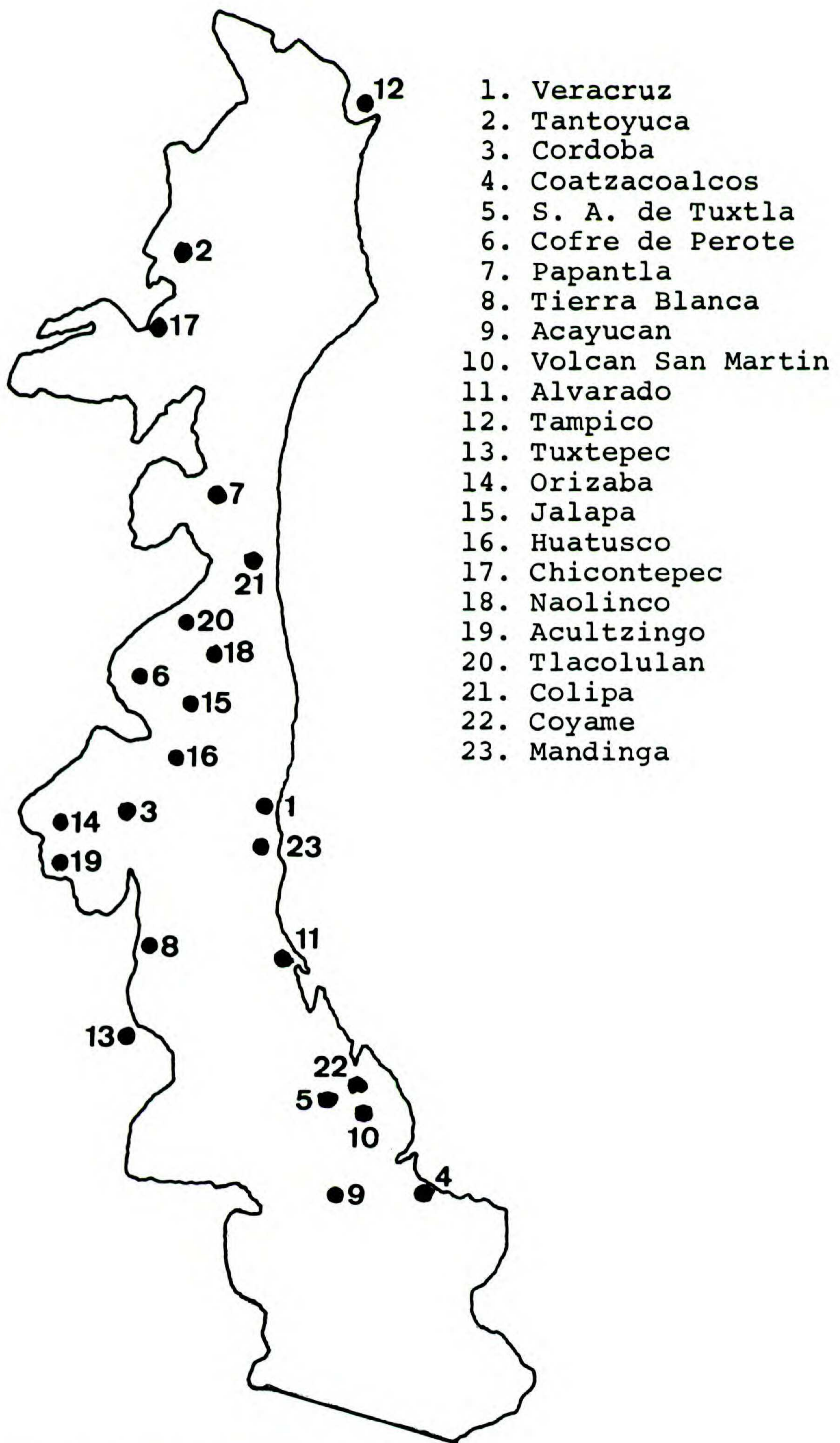


FIGURE 1. State of Veracruz, index map of place names.

around Tierra Blanca (3,500–4,000 mm). The driest areas are on the western slopes of the west-central mountainous zone, in the northernmost portion of the state, created by the Sierra de Tamaulipas; in the region inland from the port of Veracruz, created by the Sierra de Chiconquiaco; and on the west side of the Sierra de los Tuxtlas in the south-central portion of the state (800–1,200 mm annually). Depending on the distribution of rainfall, regions in Veracruz have uniform precipitation (with at least about 18% of the rain falling during the dry season of December through May) or summer rains (with less than about 18% falling during the dry season). The seasonal rainfall is controlled by the trade winds (bringing summer rains), but in some regions summer rains are supplemented by winter precipitation from polar air masses (nortes) to produce a more uniform yearly rainfall. The distribution of rainfall is a visibly important factor in determining the aspect and composition of vegetation in Veracruz. The occurrence of evergreen, semievergreen, and deciduous selvas is in part a reflection of the degree and extent of the dry winter season.

In low-lying coastal areas in the north (e.g., just south of Tampico), and at higher elevations inland (e.g., Jalapa, Acayucan) fog is common (80–100 days per year). In the latter region is the vegetation, occupying mid-altitude temperate zones along the eastern escarpment, commonly referred to as cloud forest.

In the immediate vicinity of the collecting localities at Coatzacoalcos the average annual temperature is between 22 and 26°C. The minimum temperature recorded during the past 50 years is 10°C. Rainfall is about 3,000 mm annually with winter rain accounting for about 10–18% of the total. The monthly distribution of rainfall is: January, 134 mm; February, 72; March, 57; April, 51; May, 112; June, 267; July, 233; August, 297; September, 500; October, 525; November, 282; December, 195. Other aspects of the climates of Veracruz have recently been summarized by Gómez-Pompa (1973).

MODERN VEGETATION

One of the most difficult aspects of vegetational history studies in tropical regions is sorting miscellaneous genera identified from fossil microfloras into communities corresponding, as far as possible, to modern associations. Information available on modern vegetation types and their distribution, composition, and ecological parameters is essential to the reconstruction of paleocommunities and paleoenvironmental interpretations. The initial phase of Studies in Neotropical Paleobotany concerns Mexico, Panama, and Puerto Rico partly because through several current research projects the vegetation of these countries is sufficiently well known to allow recognition and characterization of communities.

A survey of Mexican vegetation reveals some modern associations well represented in Veracruz during the upper Miocene, while other climatically and geographically distinct types are absent. In the following discussion genera marked with an asterisk (*) are represented by fossil pollen in the upper Miocene Paraje Solo Formation of Veracruz. Various pollen types of the stenopalynous Cyperaceae, Gramineae, Chenopodiaceae-Amaranthaceae, and Com-

positae could not be generically identified. Pollen of the large and important tropical plant family Lauraceae is destroyed by standard processing techniques and presumably does not fossilize.

GENERAL VEGETATION OF MEXICO

The modern vegetation of Mexico is known through floristic studies (Shreve & Wiggins, 1964, Sonora; Rzedowski, 1961, San Luis Potosí; Rzedowski & McVaugh, 1966, Nueva Galicia; Breedlove, 1973, Chiapas), monographs (Clausen, 1959, *Sedum*; Martínez, 1963, Pinaceae; Gentry, 1972, Agavaceae), and maps (Leopold, 1950). The most recent summary of Mexican vegetation is the map and accompanying text, *Tipos de Vegetación de la Republica Mexicana* (Flores Mata, et al., 1971), and the *Guías Botánicas de Excursiones en México* (Sociedad Botánica de México, 1972).

Following terminology used in the *Tipos de Vegetación*, the primary vegetation of Mexico is classified into 25 principal types.

Vegetación Hidrofila.—

(1). *Manglar*—Mangrove swamps of *Rhizophora** *mangle* L., *Avicennia germinans* L., *Laguncularia** *racemosa* (L.) Gaertn.f., and *Conocarpus erecta* L. In southeastern Mexico manglar vegetation is found along the coast and inland from Alvarado, and from Coatzacoalcos continuing around coastal Yucatán Peninsula.

(2). *Popal*—Herbaceous, fresh-water marsh vegetation characterized by plants with large, broad leaves and anchored in relatively deep water. Important genera are *Calathea*, *Thalia*, *Leersia*, *Paspalum*, *Panicum*, *Oryza*, *Zizaniopsis*, and *Hymenachne*. Popal vegetation occurs scattered along the southeastern coast (e.g., just southwest of Coatzacoalcos) and is especially well developed in an extensive area around Bahía Ascención, eastern coastal Yucatán.

(3). *Tular y Carrizal*—Reed-Sedge marshes of *Phragmites australis* (Cav.) Trin. ex Steud., *Scirpus californicus* (Meyer) Steud., *Cyperus giganteus* Vahl, and *Typha*. Sedge and reed marshes are locally developed around Lago Texcoco and in lowlands east of Toluca, and scattered throughout southeastern Mexico.

(4). *Palmar*—Palm stands along the coast in warm to hot climates. The common genera include *Scheelea*, *Orbignya*, *Sabal*, *Pseudophoenix*, *Paurotis*, *Brahea*,* *Roystonea*, *Washingtonia*. In southeastern Mexico there are extensive palm stands inland from Alvarado, and smaller scattered communities around Coatzacoalcos, Villahermosa, and along the Río Usumacinta.

(5). *Sabana*—Savannas of *Byrsonima crassifolia* (L.) DC., *Curatella americana* L., *Crescentia alata* H.B.K., *C. cujete* L., and understory grasses of *Andropogon*, *Paspalum*, *Trichachne*, *Imperata*, *Trachypogon*, and *Manisuris*. Extensive savannas occur just to the north of Palenque and Pichucalco, and between Tuxtepec and San Andrés Tuxtla.

Selva.—Arborescent vegetation of warm tropical lowlands and generally with several to many common tree species (a "multidominant" community).

(6). *Alta Perennifolia* (High Evergreen Selva)—Association of tall evergreen trees (commonly over 30 m) and associated understory vegetation. This

community is frequently referred to as "the tropical rainforest." In Mexico characteristic species include *Terminalia** *amazonica* (J. F. Gmelin) Exell, *Swietenia macrophylla* King, *Brosimum alicastrum* Swartz, *Vochysia hondurensis* Sprague, *Andira galeottiana* Standley, *Bernoullia flammea* Oliver, *Dialium guianense* (Aubl.) Sandwith, *Calophyllum brasiliense* Camb., *Pseudolmedia oxyphyllaria* Donnell Smith, *Calatola laevigata* Standley, *C. mollis* Standley, *Talauma mexicana* (DC.) G. Don, *Ficus tecolutensis* (Liebm.) Miq., and species of *Inga* and *Quercus*.*

(7). *Alta Subperennifolia* (High Semi-Evergreen Selva)—In this community 25–50% of the trees are deciduous during the dry season. Characteristic species include *Brosimum alicastrum* Swartz, *Manilkara zapota* (L.) v. Royen, *Mastichodendron capiri* (A. DC.) Cronquist, *Swietenia macrophylla* King, *Bucida buceras* L., *Mirandaceltis monoica* (Hemsley) Sharp, *Carpodiptera ameliae* Lundell. An example of this community occurs in southern Yucatán near the Guatemalan border.

(8). *Mediana Subperennifolia* (Medium Semi-Evergreen Selva)—This community has many species in common with the High Semi-Evergreen Selva, occupying areas of slightly less rainfall. It is defined by trees 15–30 m tall with 25–50% deciduous during the dry season. In southeastern Mexico the community once occupied extensive lowland areas to the north (Tampico to the Orizaba-Córdoba region) and south of Veracruz-Tabasco in the Yucatán lowlands.

(9). *Mediana Caducifolia* (Medium Deciduous Selva)—Trees 15–30 m tall with more than 75% deciduous during the dry season. Common species include *Hymenaea courbaril* L., *Enterolobium cyclocarpum* (Jacq.) Griesb., *Cedrela** *odorata* L., *Licania arborea* Seem., *Tabebuia chrysantha* (Jacq.) Nicholson, and *Hura polyandra* Baill. In southeastern Mexico remnants of this selva occur along a broad zone between Campeche northeast to Cabo Catoche.

(10). *Baja Subperennifolia* (Low Semi-Evergreen Selva)—Trees less than 15 m tall and 25–50% of the trees deciduous during the dry season. Characteristic species include *Acacia** *pennatula* (Schlecht. & Cham.) Benth., *Acrocomia mexicana* Karw., *Haematoxylum campechianum* L., *Bucida buceras* L., *Metopium brownei* (Jacq.) Urban, and species of *Ateleia*, *Vitex*, *Lonchocarpus*, and *Coccoloba*.* In the Tipos de Vegetación the Baja Subperennifolia is shown as scattered isolated stands in southern Yucatán. Breedlove (1973: 159–160) uses "Short-tree Savanna" for comparable vegetation in Chiapas.

(11). *Baja Caducifolia* (Low Deciduous Selva)—Trees less than 15 m tall and almost all deciduous during the dry season. Members of this community include *Lysiloma bahamensis* Benth., *Cordia dodecandra* DC., *Alvaradoa amorphoides* Liebm., *Haematoxylon brasiletto* Karst., *Ceiba acuminata* (S. Watson) Rose, *Bursera** *excelsa* (H.B.K.) Engl., *Pistacia mexicana* H.B.K., *Amphipterygium adstringens* (Schlecht.) Schiede, *Cyrtocarpa procera* H.B.K., *Conzattia sericea* Standley, *Pithecellobium flexicaule* (Benth.) Coult., *Olneya tesota* Gray, *Idria columnaris* Kellogg, and *Cercidium*. In southeastern Mexico low deciduous selvas are found in the vicinity of Veracruz and in northern Yucatán Peninsula.

Bosque—Arborescent vegetation of cool, temperate, moderate to high altitudes, generally with one to few dominant tree species.

(12). *de Oyamel*—Coniferous forests of *Abies*.* These are high altitude forest scattered through the mountains of southern Mexico. In southeastern Mexico *Abies religiosa* (H.B.K.) Schlecht. & Cham. is found between Mexico City and Puebla, near Perote, and in the Orizaba-Córdoba region.

(13). *de Cedro y Tásate* (*Cupressus* and *Juniperus* Woodlands)—This community is not extensive in Mexico, but some stands are found just to the northeast of Iguala, and near Perote.

(14). *de Pino* (Pinelands)—This is also a high altitude community, and more or less pure stands of *Pinus** are of scattered and isolated distribution. Examples occur between Mexico City and Puebla, and in the Orizaba-Córdoba region.

(15). *de Pino-Encino* (Pine-Oak Woodlands)—The pine-oak woodlands are among the most widespread of plant communities in Mexico. With differing species composition and proportion of *Pinus** to *Quercus**, this community occurs at higher elevations ranging from northern Baja California-Arizona-Texas borders southward to Guatemala.

(16). *Caducifolio* (Deciduous Forests)—These forests occur in temperate and humid areas at elevations between 1,000 and 2,000 m along the eastern slopes of the Sierra Madre Oriental from northwest of Ciudad Mante south to the Guatemalan border. Characteristic genera include many disjunct to varying degrees from the deciduous forest of eastern United States, as *Liquidambar**, *Quercus**, *Nyssa*, *Carpinus*, *Ostrya*, *Fagus*, *Tilia*, *Cornus*, *Myrica**, *Ilex**, *Juglans**, *Ulmus**, *Populus**, in addition to *Ternstroemia*, *Oreopanax*, *Bocconia*, *Engelhardtia**, *Meliosma**, *Podocarpus**, *Cleyera**, *Cyathea**, *Eugenia**, *Tournefortia**, *Guarea**, *Hedyosmum**, *Justicia**, *Struthanthus**, *Lycopodium**, *Selaginella**, *Psilotum**, *Alsophila**, *Dichapetalum**, and *Weinmannia*.

(17). *de Encino* (Oak Forests)—This community is also widespread from arid zones to the tropics involving different species of *Quercus**. In southeastern Mexico oak woodlands are found east of Tuxtepec, just east of Coatzacoalcos inland toward San Andrés Tuxtla, and at the Veracruz-Oaxaca border in the Isthmus of Tehuantepec.

(18). *Mezquital*—Mesquite (*Prosopis*) shrub vegetation of northern (along the Texas-Arizona border) and central (Guanajuato-Querétaro region) Mexico.

(19). *Chaparral*—This is a shrub community common in northern Mexico frequently found at lower elevations of mountainous regions at the contact with arid flat lowlands. Characteristic genera are *Quercus**, *Arctostaphylos*, *Cercocarpus*, *Amelanchier* and *Adenostoma*.

Matorral.—Thicket.

(20). *Submontano* (Submontane Thicket)—Vegetation of low trees 3–5 m tall, briefly deciduous during the dry season, occurring in arid regions of northeastern Mexico. The principal genera include *Leucaena*, *Cordia*, *Bumelia*, *Heliopsis*, *Acacia**, *Opuntia*, *Gochnatia*, *Celtis**, *Flourensia*, *Mimosa**, *Colubrina*, *Lysiloma*, *Pseudomoringium*, *Pistacia*.

(21). *Crasicuale*—A community characterized by large cylindrical or flat-stem cacti of *Lemaireocereus*, *Neobuxbaumia*, *Myrtillocactus*, *Escontria*, *Car-*

negia, *Cephalocereus*, and *Opuntia*. In south-central Mexico the Matorral Crasicaule is especially well developed along the Tehuacán Valley between Huajuapán de León and the city of Tehuacán.

(22). *Desértico Rosetófilo*—A community of dry regions with plants of rosette growth form. Genera include *Yucca*, *Agave*, *Hechtia*, *Dasyllirion*, *Beau-carnea*, and *Nolina*. An example of the Matorral Desertico Rosetofilo is found in south-central Mexico just north of Tehuacán.

(23). *Desértico Micrófilo*—A vegetation type found in dry areas and characterized by plants with small leaves. Common genera include *Larrea*, *Flourensia*, *Allionia*, and *Celtis*.*

Zacatal.—Grasslands.

(24). *Pastizal*—Dry grasslands of central and northern Mexico consisting of *Bouteloua*, *Muhlenbergia*, *Sporobolus*, *Hilaria*, *Distichlis*, *Lycurus*, *Heteropogon*, *Elyonurus*, *Buchloe*, *Eragrostis*, *Spartina*, *Cathestecum*, and *Opizia*.

(25). *Zacatonal*—Grasslands of colder higher elevations with more robust grasses of *Muhlenbergia*, *Festuca*, *Stipa*, and *Calamagrostis*.

VEGETATION OF VERACRUZ

The modern vegetation of Veracruz is known through several regional studies (e.g., Gómez-Pompa, 1966; Gómez-Pompa et al., 1964; Gómez-Pompa & León Cázares, 1970; León Cázares & Gómez-Pompa, 1970), and has recently been summarized by Gómez-Pompa (1973). He recognizes 22 communities, and in the following summary these are correlated with the classification terminology used in the *Tipos de Vegetación*.

Forests (Bosques).—

(1). *Needle-Leaved Forests* (Bosque de Oyamel, de Pino, de Pino-Encino) and *Scale-Leaved Forests* (Bosque de Cedro y Tásate)—These are high-altitude coniferous forests at elevations between 3,000 and 4,000 m, with an average annual temperature of about 4–11°C. The dominant species is *Pinus** *hartwegii* Lindl., with *P. montezumae* Lamb. and *Abies** *religiosa* (H.B.K.) Schlecht. & Cham. Stands are found at the Pico de Orizaba and in the Cofre de Perote. Fossil pollen of *Picea*,* not present in the modern flora of Veracruz, occurs in the Paraje Solo Formation and probably grew in the higher altitude portions of the Needle-Leaved Forest. Fossil pollen of a few wide-ranging plants that reach into the Needle-Leaved Forest, such as *Alnus** and *Smilax*,* has also been recovered.

At lower elevations of 2,000–3,000 m, pine is mixed with *Quercus** to form the wide-spread Bosque de Pino-Encino. Gómez-Pompa (1973: 95) gives a climatograph from Acultzingo showing an average annual temperature of 17.4°C (minimum ca. 13°C) and a yearly rainfall of 723.7 mm. The pine species are *P. pseudostrobus* Lindl., *P. teocote* Cham. & Schlecht., *P. rudis* Endl., *P. strobus* L. var. *chiapensis* Martínez, *P. oocarpa* Schiede, *P. ayacahuite* Ehrenberg, *P. leiophylla* Schlecht. & Cham., and *P. patula* Schlecht. & Cham. The common

species of oak are *Q. candicans* Nee, *Q. xalapensis* Humb., *Q. castanea* Nee, *Q. crassifolia* Humb., *Q. mexicana* Humb., and *Q. excelsa* Liebm. Associated with the *Quercus-Pinus* Forest are two genera represented by pollen in the Paraje Solo Formation, *Alnus** *arguta* (Schlecht.) Spach, and *Smilax spinosa* Mill.

A small scale-leaved forest of *Juniperus deppeana* Steud. occurs near Perote. This is a community of drier climates, found near the contact of temperate pine-oak and more arid vegetation at about 2,500 m. Other species include *Pinus cembroides* Zucc., *Nolina parviflora* (H.B.K.) Hemsley, *Quercus microphylla* Nee, and *Sophora secundiflora* (Ortega) Lag. At present, pollen of *Juniperus*, *Nolina* and *Sophora* has not been found in the Paraje Solo microflora.

(2). *Broad-Leaved Forests* (Bosque de Encino)—These forests are commonly dominated by *Quercus*.* At higher elevations they grade into pine-oak communities, but in warm lowlands they constitute a more distinct community. The principal species is *Q. oleoides* Cham. & Schlecht. Also present are other plants also represented by pollen in the Paraje Solo Formation, including *Alchornea** *latifolia* Swartz, *Sapium** *lateriflorum* Hemsley, and *Coccoloba** *barbadensis* Jacq.

(3). *Deciduous Forests* (Bosque Caducifolio)—Gómez-Pompa (1973: 102) provides a climatograph from Huatusco, elevation 1,344 m, within the Deciduous Forest. The temperature range is from 15°C (December–January) to 21°C (May–June), with an annual average of 15.7°C. Yearly rainfall is 1,745 mm, falling mainly from April through October. The characteristic deciduous species is *Liquidambar** *macrophylla* Oerst. mixed with *Quercus** (*Q. affinis* Schwidw., *Q. ocoteaefolia* Liebm., *Q. skinneri* Benth., *Q. brachybotrya* Zucc., *Q. corrugata* Hook., and *Q. pilarius* Trel.). Both *Liquidambar* and *Quercus* occur in the Paraje Solo Formation together with several others presently found in the Deciduous Forest: *Cleyera** *serrulata* Choisy, *Cyathea** *fulva* (Mart. & Gal.) Fee, *Eugenia** *trunciflora* (Schlecht. & Cham.) Berg, *E. mexicana* Steud., *Ilex** *vomitaria* Ait., *Juglans** *pyriformis* Liebm., *Lycopodium** *cernuum* L., *Meliosma** *alba* (Schlecht.) Walp., *Podocarpus** *matudai* Lundell, *Tournefortia** *petiolaris* DC., *Ulmus** *mexicana* Liebm., *Guarea** *chichon* C. DC., *Engelhardtia** *mexicana* Standley, *Psilotum** *complanatum* Swartz, *Selaginella**, *Alsophila**, *Dichapetalum**, *Hedyosmum**, *Justicia** (widespread), *Populus** (riparian, widespread), and *Struthanthus**.

Selvas.—

(4). *High Evergreen Selvas* (Selva Alta Perennifolia)—In Veracruz this community occurs where annual precipitation ranges from a minimum of about 2,500 mm (2,726 mm at Coatzacoalcos, elevation 14 m) to 5,000 mm (4,439 mm at Coyame, elevation 340 m) with no pronounced dry season. Temperatures are from about 20°C (December–January) to 27°C (April–May) with a yearly average between 23–25°C. The dominant tree species are frequently 25–30 m tall and approximately 80% or more of the component species are evergreen. Characteristic members of the High Evergreen Selva are *Terminalia** *amazonica* (J. F. Gmelin) Exell, *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Swartz, *Ficus tecolu-*

tensis (Liebm.) Miq., and *Pseudolmedia oxyphyllaria* Donnell Smith. A few associated genera have been found in the Paraje Solo microflora, including *Cupania** *dentata* DC., *Guarea** *chichon* C. DC., *G. tonduzii* C. DC., *G. bijuga* C. DC., *G. glabra* Vahl, *Matayba** *oppositifolia* (Rich.) Britton, *Podocarpus** *guatemalensis* Standley, *Alchornea** *latifolia* Swartz, *Astrocaryum** *mexicanum* Liebm., *Bursera** *simaruba* (Swartz) Sarg., *Chamaedorea** *alternans* Wendl., *C. ernesti-agusti* (Wendl.) Oerst., *C. lindeniana* Wendl., *C. oblongata* Mart., *C. tepejilote* Liebm., *Hampea** *nutricia* Fryxell, *Sapium** *nitidum* (Monach.) Lundell, and *Tetrorchidium** *rotundatum* Standley.

(5). *High Semi-Evergreen Selvas* (Selva Alta Subperennifolia)—The deciduous habit of up to 50% of component species characterizes the High Semi-Evergreen Selva. The association is found in areas of slightly reduced rainfall (minimum ca. 1,800 mm per year) or in more humid areas on well-drained soils. The dominant species is frequently *Brosimum alicastrum* Swartz, with *Ficus tecolutensis* (Liebm.) Miq., *Bursera** *simaruba* (Swartz) Sarg., *Achras zapota* L., *Cedrela** *odorata* L., *Coccoloba**, *Croton nitens* Swartz, *Bernoullia flammea* Oliver, *Sapium** *lateriflorum* Hemsley, *Lonchocarpus*, *Mirandaceltis monoica* (Hemsley) Sharp, *Castilla elastica* Cerv., *Zuelania guidonia* (Swartz) Britton & Millsp., *Guarea** *chichon* C. DC., *Pithecellobium insigne* Micheli, *Tabernaemontana alba* Mill., *Iresine** *nigra* Uline & Bray, *Alchornea** *latifolia* Swartz, *Cupania** *dentata* DC., *Ilex** *condensata* Turcz., *Protium** *copal* (Schlecht. & Cham.) Engl., and *Chamaedorea** *lunata* Liebm.

(6). *Medium Semi-Evergreen Selvas* (Selva Mediana Subperennifolia)—In Veracruz this is a transition community composed of species from the tall and low selvas occupying sites intermediate between these humid and drier associations.

(7). *Low Evergreen Selva*—At the top of Volcán San Martín a low, dense vegetation with numerous epiphytes occurs (the mossy or elfin forest), composed of *Clusia*, *Elleanthus*, *Gaultheria*, *Ilex**, *Litsea*, *Monnina*, *Myrica**, *Oreopanax*, *Palicourea*, *Rapanea*, *Saurauia*, *Senecio*, and *Viburnum*. The Low Evergreen Selva is an unusual type of community with restricted distribution, and is not recognized as a distinct association in the *Tipos de Vegetación* (scale 1: 2,000,000). Other than *Ilex* and *Myrica*, which occur in several communities, elements of the elfin forest are not represented in the Paraje Solo microflora.

(8). *Low Semi-Evergreen Selvas* (Selva Baja Subperennifolia)—Agriculturally poor soils and milpa farming practices are characteristic of regions with Low Semi-Evergreen Selvas in Veracruz. Consequently, there is some uncertainty as to the naturalness of this community and the importance of anthropogenic factors in determining its range. Rainfall is relatively low (1,400–1,800 mm; Gómez-Pompa, 1973: 119–121), and the community is occasionally recognized as a type of savanna. Characteristic species are *Acrocomia mexicana* Karw., *Byrsonima crassifolia* (L.) DC., *Curatella americana* L., *Psidium guajava* L., *Crescentia cujete* L., and *Coccoloba** *barbadensis* Jacq. Only the latter occurs in the upper Miocene assemblage at Coatzacoalcos, and it ranges into other types of vegetation.

(9). *Low Deciduous Selvas* (Selva Baja Caducifolia)—These selvas occur

where precipitation is less than 1,500 mm per year, and a dry season often of six months or more is present. Most trees are less than 10 m tall and leafless during the dry season (November through March; Gómez-Pompa, 1973: 121–124). Dominant species in the Low Deciduous Selvas include *Cordia dodecandra* DC., *Crescentia alata* H.B.K., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Piscidia piscipula* (L.) Sarg., *Tabebuia chrysantha* (Jacq.) Nicholson, and *T. rosea* (Bert.) DC. None of these genera are represented by pollen in the Paraje Solo microflora. The pollen of a few genera associated with the Low Deciduous Selva (and commonly ranging into other types) has been recovered, including *Acacia** *cornigera* (L.) Willd., *A. farnesiana* (L.) Willd., *Bursera** *bipinnata* Engl., *B. fagaroides* (H.B.K.) Engl., *B. simaruba* (Swartz) Sarg., *Casearia** *nitida* (L.) Jacq., *Celtis** *iguanaea* (Jacq.) Sarg., *Comocladia** *engleriana* Loes., *Cupania** *macrophylla* A. Rich., *Daphnopsis** *brevifolia* Nevling, *Eugenia** *liebmanni* Standley, and cf. *Sapium** sp.

(10). *Low Thorn Selvas* (Matorral Submontano)—According to Gómez-Pompa (1973: 124–126): “This vegetation type is found in the driest regions of lowland areas where precipitation is under 1000 mm and where the dry season is long and pronounced. These regions also have the lowest winter temperatures in the lowlands. The combined effect of these highly selective factors gives rise to the very characteristic flora, which is a combination of floristic elements from the more humid areas in the south and the Tamaulipas deserts in the north.” Among the characteristic genera are *Abutilon*, *Acacia**, *Acanthocarpus*, *Boerhavia*, *Cordia*, *Coursetia*, *Chlorophora*, *Citharexylum*, *Croton*, *Erythroxylon*, *Eugenia**, *Guazuma*, *Jacquinia*, *Malpighia**, *Mimosa**, *Morrisonia*, *Nopalea*, *Parkinsonia*, *Phyllanthus*, *Plumbago*, *Pithecellobium*, *Randia*, *Solanum*, *Schoepfia*, *Trichilia*, and *Zyzyphus*.

(11). *Palm Stands* (Palmar).—Three genera dominate the principal palm stands in Veracruz, *Scheelea liebmanni* Becc., *Sabal mexicana* Mart., and *Paurotis wrightii* (Griseb. Wendl.) Britton. None of these have been found as yet in the Paraje Solo microflora. Genera commonly associated with the palm stands are *Albizzia*, *Bunchosia*, *Citharexylum*, *Cupania**, *Pleuranthodendron*, *Sapindus*, *Stemmadenia*, *Trophis*, *Pithecellobium*, *Zanthoxylum*, *Ruprechtia*, *Randia*, and *Acacia**. Although six types of palm pollen have been distinguished in the microfossil assemblage (Table 1), neither individually nor collectively do they reach percentages that would reflect palm-dominated vegetation in the immediate vicinity.

Grasslands (Zacatal).—

(12). *Savannas* (Sabana)—Most genera of grasses cannot be recognized on the basis of pollen characters, especially at magnifications of the light microscope. Consequently the various communities in which the Gramineae are prominent cannot easily be distinguished in the microfossil record. At Site 4 grass pollen reaches the highest percentages (sample 19, 27%; sample 21, 45%; sample 30, 29%; sample 33, 30%). One community in which grasses may reach these percentages is the savanna. León Cázares & Gómez-Pompa (1970) describe a savanna near Coatzacoalcos. The dominant grass is *Paspalum pecti-*

natum Nees, and the common shrub is *Curatella americana* L. In the Short-Tree Savanna described by Breedlove (1973: 159–160) from Chiapas, the common trees and shrubs are *Byrsonima crassifolia* (L.) DC., *Crescentia cujete* L., *C. alata* H.B.K., and *Curatella americana* L. Other nongrass genera include *Piscidia*, *Alvaradoa*, *Kyllinga*, *Acisanthera*, *Ageratum*, *Cassia*, *Chamaesyce*, *Cococypselum*, *Cologania*, *Conostegia*, *Crotalaria*, *Diodia*, *Euphorbia*, *Hibiscus*,* *Hyptis*, *Melochia*, *Mimosa*,* *Myrica*,* *Paurotis*, *Polygala*, *Rhynchanthera*, *Russelia*, *Sauvagesia*, *Spermacoce*, *Schultesia*, *Xyris*, and *Zexmenia*. The poor representation of genera in the microflora, other than grasses, characteristic of savannas suggest this type of community was not prominent in the vicinity during the upper Miocene.

(13). *Temperate Grasslands*—Because of the agricultural practices of sedentary populations occupying the lowlands of Veracruz for at least 5,000 years, grasslands (like savannas and palm stands) are highly modified. At present natural Temperate Grasslands are poorly represented in Veracruz, but the Valley of Perote may have supported such a community in earlier times (Gómez-Pompa, 1973: 132). Remnants of a Temperate Grassland are reflected by the presence of *Bouteloua curtipendula* (Michx.) Torr., *B. gracilis* (H.B.K.) Lag. ex Steud., *Microchloa kunthii* Desv., and *Setaria geniculata* (Lam.) Beauv. Nongrass genera associated with remnants of Temperate Grasslands are *Anthericum*, *Asclepias*, *Bulbostylis*, *Cologania*, *Commelina*, *Cyperus* (Cyperaceae*), *Eryngium*, *Heliotropium*, *Ipomoea*, *Nemastylis*, *Ophioglossum*, *Oxalis*, *Piranopappus*, *Quercus*,* *Ranunculus*, *Selaginella*,* *Sisyrinchium*, *Stevia*, *Tridax*, and *Verbena*.

(14). *Saline Grasslands*—These communities may be temperate and upland, with high salinity due to evaporation, or lowland and coastal periodically inundated by marine waters. The former are characterized by *Distichlis spicata* L., and the latter by *Spartina* (*S. alterniflora* Loisel., *S. spartinae* (Trin.) Merr.; the “espartal”). Associated genera are *Actinella*, *Alternanthera* (Amaranthaceae; represented as ChenoAm.*), *Aphanostephanus* (Compositae*), *Atriplex*, *Croton*, *Cuscuta*, *Dichondra*, *Erodium*, *Gomphrena*, *Heliotropium*, *Houstonia*, *Plantago*, *Sanvitalia*, *Verbena*, *Batis*, *Borrchia*, and *Salicornia*.

(15). *Nolina-Hechtia-Agave Desert* (Matorral Desértico Rosetófilo).—Evidence for arid or semiarid vegetation during the upper Miocene is meager for southern Veracruz. In the north near the border with Puebla, at an elevation of about 23 m, there is a desert of *Nolina parviflora* (H.B.K.) Hemsley, *Hechtia roseana* L., and *Agave obscura* Schiede. Average annual temperature is 14.9°C, with extremes of about 11°C (December–January) to 16°C (May–June). Other genera are *Adolphia*, *Aneilema*, *Aristida*, *Chrysactenia*, *Bouvardia*, *Dalea*, *Dasy-lirion*, *Dyssodia*, *Juniperus*, *Loeselia*, *Lycurus*, *Mamillaria*, *Salvia*, *Stipa*, and *Tradescantia*. With the possible exception of generically undifferentated members of the Gramineae and Compositae none of these dominant (*Nolina*, *Hechtia*, *Agave*) or associated genera are presently known from the Paraje Solo Formation.

(16). *Thorn Scrub* (Matorral Crassicaule).—Two types of thorn scrub occur in Veracruz, one at higher elevations (1,500 m or more) and another less well defined one in the lowlands (less than 500 m; Gómez-Pompa, 1973: 137).

Characteristic genera in the former are *Agave*, *Asclepias*, *Bouvardia*, *Buddleia*, *Croton*, *Echinocactus*, *Eupatorium*, *Juniperus*, *Karwinskia*, *Mammillaria*, *Myrtillocactus*, *Notholaena*, *Opuntia*, and *Quercus*.* In the latter are *Bursera*,* *Caparis*, *Capraria*, *Condalia*, *Esenbeckia*, *Karwinskia*, *Nopalea*, *Prosopis*, *Pithecellobium*, *Randia*, *Yucca*, and *Zanthoxylum*. With the possible exception of the wide-ranging *Quercus* (represented in the thorn scrub by *Q. eduardii* Trel.) and *Bursera* [represented by *B. simaruba* (Swartz) Sarg.], and generically undifferentiated Compositae, none of the above have been recovered as yet from the Paraje Solo microflora.

(17). *Swamp Vegetation*.—Two types of swamp communities are present in Veracruz. One is the Inland Swamp occurring in fresh-water environments, and the other is the coastal brackish Mangrove Swamp.

(18). *Inland Swamps* (Popal)—The composition of the Inland Swamp varies and community names are based on the local dominant. A common member is *Thalia geniculata* L. (popal), associated with *Bactris*, *Cyperus* (Cyperaceae*), *Eleocharis*, and *Pontederia*.

(19). *Mangrove Swamps* (Manglar)—Deposition of the Paraje Solo sediments took place in or near a coastal, marine-brackish water environment, as evidenced by the abundance of *Rhizophora** and *Laguncularia** pollen. Modern members of the mangrove swamp include *Rhizophora mangle* L., *Laguncularia racemosa* (L.) Gaertn. f., *Avicennia germinans* L., and *Conocarpus erecta* L. Pollen of *Avicennia* and *Conocarpus* have not been identified as yet from the Paraje Solo Formation, but, even in modern communities, all four mangroves are not consistently present. Vázquez (1971), for example, did not find *Conocarpus* in mangrove swamps near Mandinga, Veracruz.

Another vegetation type, intermediate between the fresh-water Inland Swamps and the brackish Mangrove Swamps, is one characterized by *Pachira aquatica* Aubl. These communities are mainly inland but can tolerate occasional inundation and slightly brackish waters. Associated genera include *Acrostichum*, *Amerimon*, *Annona*, *Avicennia*, *Clerodendrum*, *Dalbergia*, *Diospyros*, *Ficus*, *Hibiscus*,* *Laguncularia*,* *Pithecellobium*, *Piper*, *Randia*, *Rhabdadenia*, *Rhizophora*,* and *Sapium*.*

The *Thalia* and *Pachira* swamps are of local and scattered occurrence in Veracruz. Their restricted distribution, together with generally low pollen production, presence of stenopalynous grasses, sedges, composites, and chenopods, and the poorly developed exine of some species may account for their low numerical representation in sediments deposited under coastal marine-brackish water conditions. In contrast, *Rhizophora* (maximum 96%) and *Laguncularia* (maximum 56%) produce moderate to large amounts of pollen and being locally dominant are over-represented considering the regional vegetation of southern Veracruz.

(20). *Paramo Vegetation* (Zacatonal).—The Paramo is a high-altitude community between timber line and the zone of permanent snow. Since the Paraje Solo sediments were deposited at sea level, the absence of pollen of Paramo

genera, like elements of the *Thalia* and *Pachira* swamps, is not significant. Paleobotanical data presently available for southern Veracruz is not adequate to assess the presence or absence of these communities. The Sierra Madre Oriental reached significant heights at the end of the Cretaceous, and there is no reason to assume the absence of Paramo vegetation by the end of the Miocene. Also, swamp communities, unlike savannas and palm stands, are not as suspect of anthropogenic control or influence and were likely present at various times and places during the Cenozoic.

(21). *Coastal Dunes Vegetation*.—This community includes a number of grasses (*Andropogon glomeratus* (Walt.) B.S.P., *A. litoralis* Nash, *Eragrostis domingensis* (Pers.) Steud., *Panicum repens* L., *Paspalum vaginatum* Swartz, *Sporobolus virginicus* (L.) Kunth, *Spartinia patens* (Ait.) Muhl., *Uniola paniculata* L.), composites (*Bidens squarrosa* H.B.K., *Iva asperifolia* Less., *Palafoxia texana* DC.), sedges (*Cyperus articulatus* L., *C. ligularis* L., *Fimbristylis spathacea* Roth) and Chenopods. (*Amaranthus gregii* S. Watson). These families are well represented in the fossil microflora, but individual genera cannot consistently be distinguished on the basis of pollen characters. It is likely, however, given the depositional environment of the Paraje Solo sediments, that coastal dune and the related island vegetation (Gómez-Pompa, 1973: 143), is represented in the microflora. Other genera occurring in these communities recovered from the Paraje Solo Formation are *Acacia*,* *Casearia*,* *Coccoloba*,* *Iresine*,* *Laguncularia*,* *Terminalia*,*⁴ and *Tournefortia*.*

(22). *Aquatic Vegetation Types*.—Pollen of various elements comprising aquatic vegetation is poorly represented in the Paraje Solo microflora. Spores of the floating fern *Ceratopteris*,* and pollen of *Utricularia** have been recovered. Other genera common to the aquatic flora of Veracruz are not known from the microflora (e.g., *Halodule*, *Thalassia*, *Halophila*, *Ruppia*, *Syringodium*, *Crinum*, *Pontederia*, *Sagittaria*, *Typha*, *Nymphaea*, *Cabomba*, *Ceratophyllum*, *Najas*, *Bocopa*, and *Pistia*). This does not preclude the presence of these communities, however, since for reasons mentioned in section 20, pollen of aquatic plants are often poorly represented in lignites.

The survey of modern vegetation in Mexico serves to identify the geographic region having closest floristic similarity to the Miocene communities. Although some vegetation types are wide-ranging (e.g., Bosque de Pino y Encino), clearly, the paleocommunities represented in the Paraje Solo microflora are most similar to the modern vegetation of southeastern Mexico. Of the 69 identified genera listed in Table 1 (excluding tentative cf.-identifications), only 5 are no longer present in Veracruz (Table 4), and two of these (*Ceratopteris*, *Laetia*) are known from adjacent states. The genus *Symphonia*, known for several years in the fossil flora, has now been found in the modern vegetation (Gómez-Pompa, personal communication, 1974). Thus, the similarity in generic composition of the Paraje Solo assemblage to the present vegetation in Veracruz is

⁴ The lowland species *Terminalia catappa* L. in Veracruz is introduced.

clearly evident, and makes possible rather precise reconstruction of the paleo-communities and paleoenvironmental conditions.

AGE AND STRATIGRAPHY OF THE PARAJE SOLO FORMATION

Sediments exposed in the vicinity of Coatzacoalcos are of Cenozoic age, ranging from the Lutitas Nanchital Formation (Paleocene-Eocene) to the Acalapa Formation (Pliocene), with Quaternary sandstones and deltaic deposits from the Coatzacoalcos and Uxpanapa rivers currently being deposited along the coast and in bordering mangrove swamps. In the immediate vicinity lignites as distinct lithological units are confined to the Paraje Solo Formation as beds 2.5–20.5 cm thick in fine to coarse-grained sediments.

The Paraje Solo Formation is underlain by the Filisolo and Concepción Superior formations, and overlain by the Agueguexquite Formation:

Acalapa
Cedral
Agueguexquite
Paraje Solo
Filisolo
Concepción Superior
Concepción Inferior
Encanto
Depósito
La Laja
Lutitas Nanchital

Both the Paraje Solo and Filisolo Formations lack fossil faunas. The overlying Agueguexquite Formation was originally assigned to the upper Miocene based on benthic microfossil assemblages, and the Paraje Solo Formation was regarded as middle Miocene (Stratigraphic Chart, Petróleos Mexicanos Zona Sur; Gutiérrez Gil, pers. comm., 1964). The plant microfossils suggested a younger age, particularly in the presence of Compositae pollen of the Lactuceae type. In the southern Gulf-Caribbean region pollen of the Lactuceae does not appear in stratigraphically meaningful amounts until the upper Miocene. Its common occurrence in the Paraje Solo Formation (Figs. 86–87) at several sites (Table 1), together with the modern aspect of the total assemblage, indicated an age no older than upper Miocene. Subsequently an abundant fauna containing the planktonic *Globorotalia margaritae*, regarded as a guide fossil to the upper Miocene of southern coastal Mexico, has been found in the Concepción Superior Formation. Revision of the benthic and planktonic foraminifera of the Agueguexquite Formation has resulted in its reassignment to the basal Pliocene. This formation is separated from the underlying Paraje Solo Formation by an unconformity. Thus the stratigraphic relationships, as presently understood, place the Paraje Solo Formation, lacking a fossil fauna but containing Lactuceae pollen, between the upper Miocene Concepción Superior and the Pliocene Agueguexquite Formation, both dated on the basis of benthic and planktonic foraminifera. This suggests an age of upper to uppermost Miocene for the Paraje Solo Formation. On the basis of this revised age assignment, the pollen and spores of the Paraje Solo Formation represent remnants of a vegetation occupying southeastern coastal Mexico and the eastern slopes of the Sierra Madre Oriental approximately 10 to 12 million years ago.

MATERIALS AND METHODS

Reference Collection of Modern Taxa: Identification of plant microfossils was by comparison with modern palynomorphs in a pollen and spore reference collection. The collection numbers about 15,000 species and has been assembled through exchange and processing of herbarium material. Slides for our laboratory were processed by the KOH-acetolysis technique, mounted unstained in glycerine jelly, and sealed with diaphane. A few of the exchange slides are mounted in silicone oil. All material used for identification purposes has a voucher in one of several herbaria (A, GH, MICH, MO, TEX, US).

Sample Preparation of Fossil Material: Processing procedures for the lignites, fine-grained lignitic sandstones, and siltstones generally follow techniques described by Gray (1965). Surfaces were scraped and washed with distilled water, crushed, and sonicated for 1–3 min. The residues were rinsed in 10% HCl (for removal of carbonates), washed 6–8 times with distilled water, transferred to polyethylene beakers, and covered with HF for 12 h (removal of silicates). Following the HF treatment the samples were rinsed and covered with Schulze solution (mixture of saturated KClO_3 to equal parts of HNO_3) for 1–24 h depending on the amount of organic material present. The purpose of the Schulze solution is to oxidize lignins present in the matrix. Following oxidation, samples were treated with an acetolysis mixture (9 parts of acetic anhydride to 1 part of concentrated sulfuric acid) for 1–3 min for removal of cellulose debris by esterification. After acetolysis, samples were rinsed in glacial acetic acid, distilled water, 50% glycerol (for swelling of compressed pollen and spores), and drained for 1 h. The concentrated pollen residues were mounted unstained in glycerine jelly and sealed with diaphane. The plant microfossils were photographed with a Zeiss microscope and automatic camera using Panatomic-X film. The microfossils are illustrated in Figs. 6–255.

THE COLLECTION LOCALITIES

The general depositional environment of the Paraje Solo lignites can be estimated from conditions presently prevailing at sites of comparable sedimentation. Studies of peat deposition in warm-temperate regions (e.g., Scholl, 1964a, 1964b; Cohen & Spackman, 1972) indicate that the peat precursors of lignites dominated by mangroves (*Rhizophora*, *Laguncularia*, *Avicennia*, *Conocarpus*, *Pelliciera*) are paralic (marine coastal) and frequently form under deltaic environments. Freshwater streams emptying into ocean waters create the brackish conditions favorable to mangrove vegetation. In southern Veracruz these conditions are provided by the major drainage systems of the ríos Papaloapan, Coatzacoalcos, Uxpanopa, and Tonalá emptying into the Gulf of Mexico in the vicinity of Coatzacoalcos. This is generally a low-energy type of environment with regards to sediment transport where autochthonous peat and fine-grained sediments can accumulate. The accumulation of these sediments is favored by a broad, low, relatively flat coastal plain that extends along the coast of Veracruz. Relatively slight eustatic changes in sea level or local uplifts and subsidence associated with vulcanism (e.g., rise of the Sierra de Los

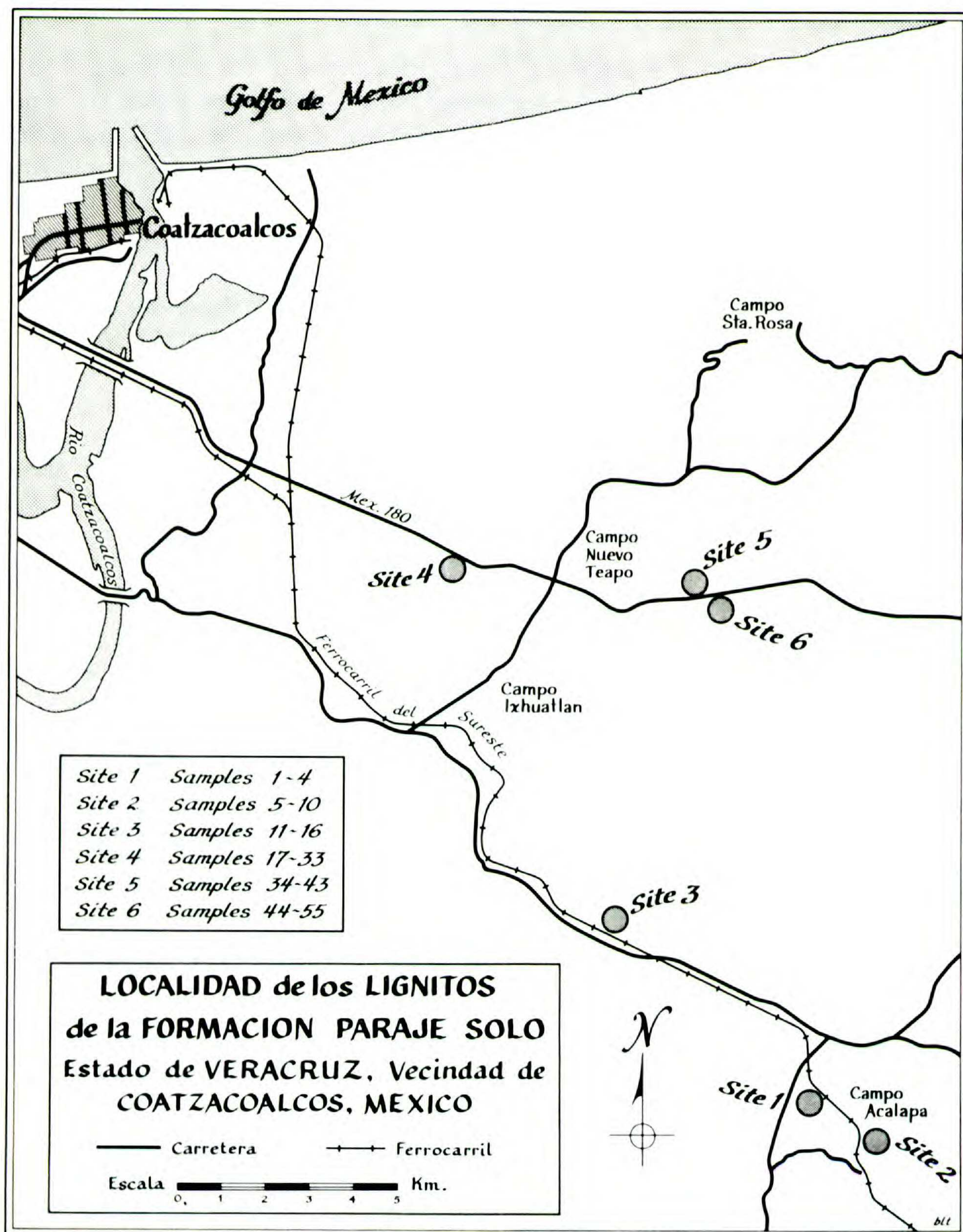


FIGURE 2. Map of collecting localities in the upper Miocene Paraje Solo Formation near Coatzacoalcos, Veracruz, Mexico.

Tuxtlas near Coatzacoalcos) affect extensive inland areas of the coastal plain. Marine transgressions depositing coarser-grained sandstones, occasional pirating of coastal sections of drainage systems, and marine invasion of paludal (swamp) environments are characteristic of mangrove habitats. In areas at and just beyond high tide some evaporation of interstitial water results in gypsum and other evaporites being incorporated into the accumulating sediments.

The sediments of the Paraje Solo Formation consist of micaceous and ferruginous (limonitic) clays, silts, fine- to medium-grained sandstones, organic debris (lignites), volcanic ash, and gypsum. This lithology is consistent with the low-lying, coastal, warm-temperate, brackish-water environments of modern mangrove peat accumulation generally, and the local volcanic supplements of the Coatzacoalcos region.

Samples were obtained from six exposures of the Paraje Solo Formation located SSE of Coatzacoalcos, Veracruz, Mexico (Fig. 2). Collections were made along the Ferrocarril del Sureste (sites 1, 2, 3) and from roadcuts along Mexico 180 (sites 4, 5, 6). The localities cover an area of approximately 20 km (between sites 2 and 4) by 8 km (between sites 3 and 5) at 18°20'N latitude and 95°N longitude.

SITE 1

This site was along a small bank on the W side of the railroad at km marker 34.4. The base of the section was a grey micaceous siltstone, with organic debris, measuring 0.6 m from the base to an overlying layer of highly organic (lignitic) siltstone. Sample 1 was obtained from the lower siltstone. Preservation was poor and fewer than 50 grains per slide were encountered. Thick-walled monolet fern spores were most abundant, and total spores constituted 65% of the sample (Table 1), possibly reflecting differential preservation.

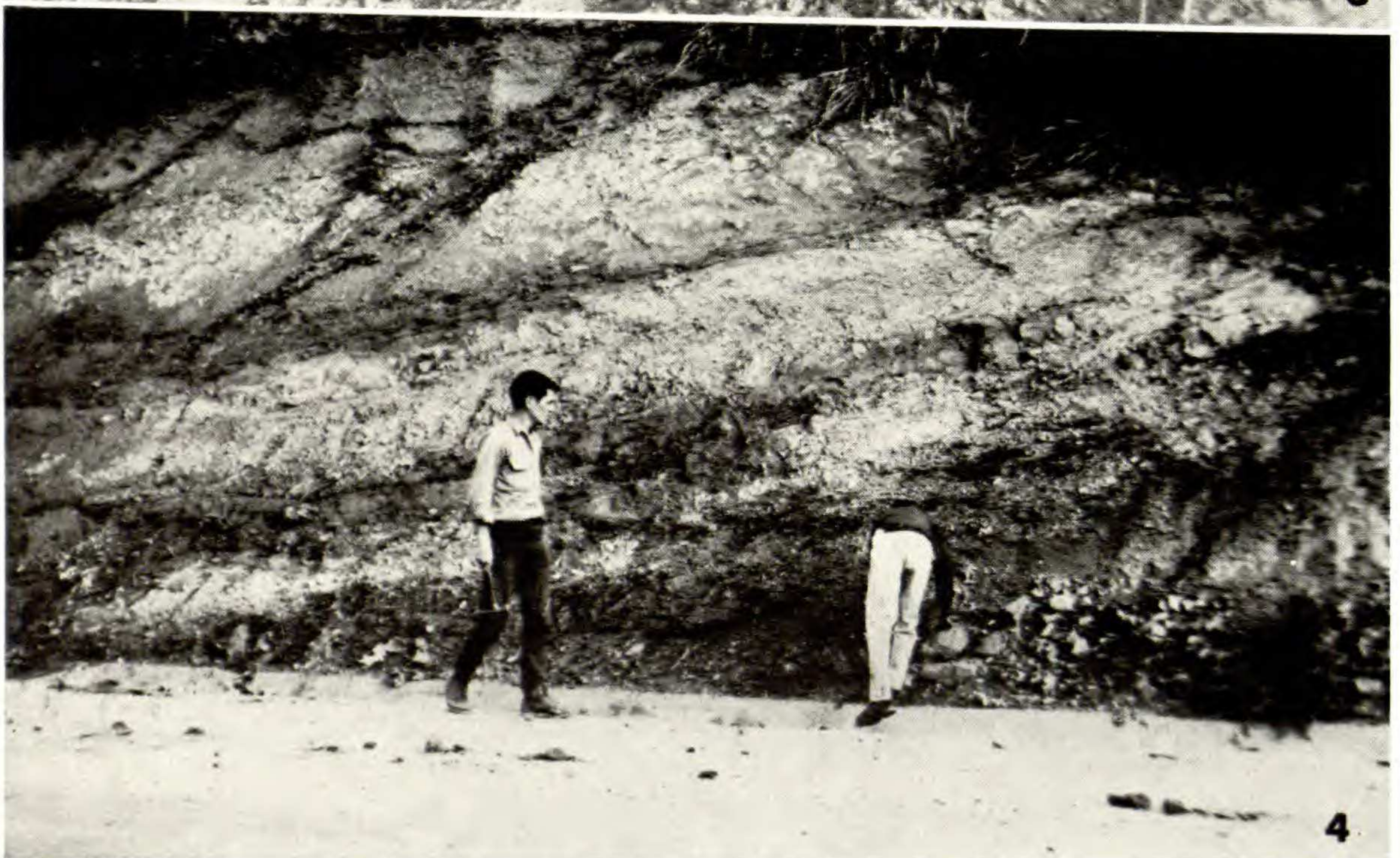
Above the siltstone was a lignitic siltstone 10 cm thick, containing well-preserved plant microfossils, from which sample 2 was obtained. Overlying the lignitic siltstone was a 10 cm layer of fine-grained sandstone. Sample 3 from this sandstone was barren. Above the sandstone was 8 cm of a conspicuous layered lignite (sample 4) and a good pollen and spore flora was recovered.

SITE 2 (Fig. 3)

This site is 1.6 km SE of site 1 at km marker 36. Sample 5 was collected from a basal grey mudstone and contained a greater diversity of palynomorphs than the approximate stratigraphically equivalent layer at site 1 (sample 1). Sample 6 was a grey muddy siltstone with quartz particles collected 15 cm above sample 5. Sample 7 was 15 cm above sample 6. Sample 8 was from the siltstone 25 cm above sample 7. Sample 9 was taken from the grey siltstone. Sample 10 was taken from a buff-colored, muddy clay siltstone with higher organic content than samples 5–9 and with a more diverse microflora.

SITE 3

This site was a south-facing bluff at km marker 28, 5.6 km NW of site 1. The locality was at the settlement of Trancas Viejas, opposite the entrance to the Pemex locality Moloacan Noreste #2. Samples 11–16 were collected, but only numbers 13 and 15 contained pollen and spores. Sample 13 was a medium brown siltstone, highly organic, ferruginous and micaceous. Above sample 13 was a 10 cm layer of sandstone from which sample 14, barren of pollen and



FIGURES 3–4. Collecting localities for lignites in the upper Miocene Paraje Solo Formation, vicinity of Coatzacoalcos, Veracruz, Mexico. Field associates are Mr. David Jarzen and Mr. Enrique Martínez-Hernández (January 30, 1967).—3. Site 2.—4. Site 5.

spores was obtained. Above the sandstone was a 5 cm layer of a dark-brown silty lignite. Sample 15 was taken from the lignite.

SITE 4

Site 4 is approximately 8.5 km NNW of site 3, and about 16 km from sites 1 and 2. The localities are exposed along a roadcut of Mexico 180 on the S

side of the road. Samples 17–26 (bottom to top) were obtained at 30 cm intervals from a channel cut, and samples 28–33 from a parallel channel cut 6 m W along the same roadcut. From the first group, samples 17, 19, 21, and 25 contained plant microfossils, and from the second group, samples 30, 32, and 33. The lithology and stratigraphic relationships between these samples are given below:

<i>East Channel Cut</i>	6 m <i>West Channel Cut</i>
Sample 25, light buff-colored, moderately organic siltstone		
Sample 21, dark brown lignitic siltstone		Sample 33, dark brown lignitic siltstone
		Sample 32, thin lignitic siltstone
Sample 19, brown lignitic siltstone		Sample 30, brown lignitic siltstone
Sample 17, light buff-colored moderately organic siltstone		

SITE 5 (Fig. 4)

This locality is 6 km E of site 4 on the N side of Mexico 180. The section consists of lignites and fine-grained lignitic siltstones. Samples 34–43 were collected, and 34, 35, 37, 38, and 40 contained plant microfossils. Sample 34 is a light-grey siltstone and sample 35 a light buff-colored siltstone with paper-thin layers of black organic material. Samples 37 and 38 were from the bottom and top, respectively, of a 30 cm thick highly organic lignitic siltstone. Sample 40 was from a grey siltstone. Three additional collections were made in the sandstone above (samples 41–43) but all were barren or contained only poorly preserved pollen and spores.

SITE 6

This locality is 1 km E of site 5 on the S side of Mexico highway 180. In 1967 the site was adjacent to a sign designating Pemex locality Teapa Nueva Ote No. 1. Samples 44–55 were collected, and 44, 45, 49, 51, and 54 contained pollen and spores. Samples 44 and 45 were buff colored highly organic lignitic siltstones from the bottom and top of a basal lignite, sample 49 was a lignite, and samples 51 and 54 were indurated, nearly coalified lignites with a scattered surficial layer of sulfur. Samples 44, 45, and 49 contained high percentages of *Quercus*, while numbers 51 and 54 contained 86% and 91% *Rhizophora*, respectively (Table 1).

Sediment deposition in mangrove environments is rapid, and no significant time interval is likely represented in the 5–6 m distance between the lowest

TABLE 2. Taxa represented by fossil pollen and spores in the Paraje Solo Formation, Veracruz, Mexico.

Psilopsida	Burseraceae
<i>Psilotum</i>	<i>Bursera</i>
Lycopsida	<i>Protium</i>
<i>Lycopodium</i>	Chloranthaceae
<i>Selaginella</i>	<i>Hedyosmum</i>
Cyatheaceae	Combretaceae
<i>Alsophila</i>	<i>Combretum/Terninalia</i>
<i>Cyathea</i>	<i>Laguncularia</i>
<i>Hemitelia</i>	Compositae, types 1, 2, 3, 4, 5, 6
Gleicheniaceae	Dichapetalaceae
<i>Dicranopteris</i>	<i>Dichapetalum</i>
Gymnogrammaceae	Euphorbiaceae
<i>Pityrogramma</i>	<i>Alchornea</i>
Lomariopsidaceae	cf. <i>Bernardia</i>
<i>Lomariopsis (Stenochlaena)</i>	cf. <i>Sapium</i>
Parkeriaceae	cf. <i>Stillingia</i>
<i>Ceratopteris</i>	cf. <i>Tetrorchidium</i>
Polypodiaceae	cf. <i>Tithymalus</i>
Monolete Fern Spores,	Fagaceae
types 1, 2, 3, 4, 5, 6	<i>Quercus</i>
<i>Pteris</i> , types 1, 2, 3	Flacourtiaceae
Pinaceae	<i>Casearia</i>
<i>Abies</i>	<i>Laetia</i>
<i>Picea</i>	Guttiferae
<i>Pinus</i> , types 1, 2	<i>Symphonia</i>
Podocarpaceae	Hamamelidaceae
<i>Podocarpus</i>	<i>Liquidambar</i>
Araceae	Juglandaceae
<i>Spathiphyllum</i>	<i>Engelhardtia</i>
Cyperaceae	<i>Juglans</i>
Dioscoreaceae	Lecythidaceae
<i>Rajania</i>	<i>Gustavia</i>
Gramineae	Leguminosae
Liliaceae	cf. <i>Acacia</i>
<i>Smilax</i>	<i>Desmanthus</i>
Palmae	<i>Mimosa</i> (cf. <i>M. pigra</i>)
cf. <i>Astrocaryum</i>	Lentibulariaceae
cf. <i>Attalea</i>	<i>Utricularia</i>
cf. <i>Brahea</i>	Loranthaceae
cf. <i>Chamaedorea</i>	<i>Struthanthus</i>
cf. <i>Maximiliana</i> type	Lythraceae
Acanthaceae	<i>Cuphea</i>
<i>Bravaisia</i>	Malpighiaceae
<i>Justicia</i>	cf. <i>Hiraea</i>
Amaranthaceae	cf. <i>Malpighia</i>
<i>Iresine</i>	cf. <i>Mezia</i> (?) type
Amaranthaceae-Chenopodiaceae	Malvaceae
Anacardiaceae	<i>Hampea/Hibiscus</i>
<i>Comocladia</i>	Meliaceae
Aquifoliaceae	<i>Cedrela</i>
<i>Ilex</i>	<i>Guarea</i>
Betulaceae	Myricaceae
<i>Alnus</i>	<i>Myrica</i>
Boraginaceae	Myrtaceae
<i>Tournefortia</i>	<i>Eugenia/Myrcia</i>

TABLE 2. (Continued).

Onagraceae	Salicaceae
<i>Ludwigia</i>	<i>Populus</i>
Passifloraceae	Sapindaceae
<i>Passiflora</i>	<i>Allophylus</i>
Polygalaceae	<i>Cupania</i>
cf. <i>Bredemeyera</i>	<i>Matayba</i>
cf. <i>Securidaca</i>	<i>Meliosma</i>
Polygonaceae	cf. <i>Paullinia</i> (e.g., <i>P. pinnata</i>)
<i>Coccoloba</i>	cf. <i>Paullinia</i> (e.g., <i>P. turbacensis</i>)
Ranunculaceae	<i>Serjania</i>
<i>Thalictrum</i>	Sterculiaceae
Rhizophoraceae	<i>Buettneria</i>
<i>Rhizophora</i>	Theaceae
Rubiaceae	<i>Cleyera</i>
cf. <i>Alibertia</i>	Thymeliaceae
<i>Borreria</i>	<i>Daphnopsis</i>
<i>Faramea</i>	Ulmaceae
<i>Terebrantia</i>	<i>Celtis</i>
	<i>Ulmus</i>

and uppermost samples. The distribution of palynomorphs among the six sites (Table 1) does not reveal any clustering that can be related to specific stratigraphic levels or attributed to age differences between sites. The variations in pollen types and percentages more likely reflect habitat differences in this region of considerable topographic diversity. The fossil pollen and spores, therefore, are regarded as more or less contemporaneous elements of a single floral unit occupying southeastern Veracruz during a brief span of upper Miocene time.

THE MIOCENE COMMUNITIES

The reconstruction of upper Miocene vegetation in southern coastal Veracruz is based on 110 identified types of pollen and spores from the Paraje Solo Formation (Table 2), and these are arranged into paleocommunities as diagrammed in Fig. 5 (see also Table 3). Along the left and lower sides of Fig. 5 are the modern communities recognized for Veracruz by Gómez-Pompa (1973) placed according to approximate altitudinal occurrences. The generic names represent fossil pollen and spores identified from the Paraje Solo Formation. Several genera (e.g., *Rhizophora*, *Liquidambar*, *Abies*) are characteristic of specific communities (e.g., Manglar, Deciduous Forest, Needle-Leaved Forest) and these identify the principal types of associations present during the upper Miocene. Other genera range widely throughout several communities (e.g., *Alchornea*, cf. *Sapium*) and are placed in Fig. 3 according to all known principal occurrences. Three east-west transects are shown illustrating variations in the ca. 1,600 m to coastal zone vegetation in Veracruz.

Paramo vegetation presently occurs at the highest altitudes and is characterized by composites (*Cnicus*, *Gnaphalium*, *Senecio*), grasses (*Festuca*, *Muhlenbergia*, *Stipa*), and various other genera including *Asplenium* and *Draba*.

TABLE 3. Taxa of fossil pollen and spores from the Paraje Solo Formation arranged into paleocommunities, based on the composition of modern vegetation types in Veracruz. Fossil pollen of the Compositae, Cyperaceae, and Gramineae, undifferentiated generically, is present and ranges throughout most present-day communities.

Needle-Leaved and Scale-Leaved Forest (including pine and pine-oak forests):	<i>Abies</i> , <i>Picea</i> , <i>Pinus</i> , <i>Alchornea</i> , <i>Alnus</i> , <i>Quercus</i> , cf. <i>Sapium</i> , <i>Coccoloba</i> , <i>Smilax</i> , cf. <i>Stillingia</i>
<i>Cyathea</i> (in atypically low-altitude <i>Pinus strobus</i> forest near Tlapacoyan, 500 m; mixture of high selva and deciduous forest elements)	
<i>Liquidambar</i> , <i>Myrica</i> (in atypically low-altitude <i>Pinus oocarpa</i> forest on the eastern slopes of Volcán Santa Marta, 500 m; mixture of lowland and deciduous forest elements)	
Broad-Leaved (oak) Forest:	<i>Alchornea</i> , <i>Coccoloba</i> , <i>Quercus</i> , cf. <i>Sapium</i>
Deciduous (oak- <i>Liquidambar</i>) Forest:	<i>Psilotum</i> , <i>Lycopodium</i> , <i>Selaginella</i> , <i>Alsophila</i> , <i>Cyathea</i> , <i>Pinus</i> , <i>Podocarpus</i> , <i>Alchornea</i> , <i>Alnus</i> , cf. <i>Chamaedorea</i> , <i>Cleyera</i> , <i>Dichapetalum</i> , <i>Engelhardtia</i> , <i>Eugenia</i> , <i>Guarea</i> , <i>Hampea</i> , <i>Hedyosmum</i> , <i>Ilex</i> , <i>Iresine</i> , <i>Juglans</i> , <i>Justicia</i> (widespread), <i>Liquidambar</i> , <i>Meliosma</i> , <i>Myrica</i> , <i>Populus</i> (riparian, widespread), <i>Quercus</i> , <i>Struthanthus</i> , <i>Tournefortia</i> , <i>Ulmus</i>
High Evergreen Selva:	<i>Lycopodium</i> , <i>Podocarpus</i> , <i>Alchornea</i> , <i>Allophylus</i> (secondary), cf. <i>Astrocaryum</i> , <i>Bursera</i> , <i>Casearia</i> , <i>Cedrela</i> , cf. <i>Chamaedorea</i> , <i>Cupania</i> , <i>Faramea</i> , <i>Guarea</i> , <i>Gustavia</i> , <i>Hampea</i> , <i>Hibiscus</i> , cf. <i>Hiraea</i> , <i>Iresine</i> , <i>Matayba</i> , <i>Myrcia</i> , cf. <i>Paullinia</i> , cf. <i>Sapium</i> , <i>Spathiphyllum</i> , <i>Symphonia</i> , <i>Terminalia</i> , cf. <i>Tetrorchidium</i>
High Semi-Evergreen Selva:	<i>Lycopodium</i> , <i>Selaginella</i> , <i>Cyathea</i> , <i>Alchornea</i> , cf. <i>Bernardia</i> (secondary), <i>Bursera</i> , <i>Casearia</i> , <i>Cedrela</i> , cf. <i>Chamaedorea</i> , <i>Cupania</i> , <i>Daphnopsis</i> , <i>Faramea</i> , <i>Hampea</i> , <i>Hibiscus</i> , <i>Ilex</i> , <i>Iresine</i> , cf. <i>Paullinia</i> , <i>Protium</i> , <i>Quercus</i> , <i>Rajania</i> , cf. <i>Sapium</i> , <i>Securidaca</i> (secondary), <i>Spathiphyllum</i> , cf. <i>Tetrorchidium</i> , <i>Ulmus</i>
Low Evergreen Selva:	<i>Ilex</i> , <i>Myrica</i>
Low Semi-Evergreen Selva:	cf. <i>Acacia</i> , <i>Coccoloba</i> , <i>Eugenia</i>
Low Deciduous Selva:	cf. <i>Acacia</i> , cf. <i>Brahea</i> , <i>Bursera</i> , <i>Casearia</i> , <i>Celtis</i> , <i>Combretum</i> , <i>Cupania</i> , <i>Daphnopsis</i> , <i>Eugenia</i> , <i>Ilex</i> , cf. <i>Sapium</i> , <i>Comocladia</i>
Low Thorn Selva:	cf. <i>Acacia</i> , <i>Eugenia</i> , <i>Laetia</i> , cf. <i>Malpighia</i> , <i>Mimosa</i>
Palm Stands:	<i>Coccoloba</i> , <i>Cupania</i> , <i>Desmanthus</i> (secondary), <i>Palmae</i> , <i>Quercus</i>
Savanna:	<i>Coccoloba</i> , <i>Gramineae</i> , <i>Hibiscus</i> , <i>Mimosa</i> , <i>Myrica</i> , <i>Quercus</i>
Temperate Grassland:	<i>Selaginella</i> , <i>Gramineae</i> , <i>Quercus</i>
Saline Grassland:	<i>Gramineae</i>
<i>Nolina-Hechtia-Agave</i> Desert:	None
Thorn Scrub:	cf. <i>Acacia</i> , <i>Bursera</i> , <i>Quercus</i>

TABLE 3. (Continued).

Swamp/Aquatic Vegetation:

Ceratopteris, Bravaisia, Ludwigia

Mangrove Swamps:

Hibiscus, Laguncularia, Ludwigia, Mimosa (*M. pigra* type), *Rhizophora*, cf. *Sapium*, *Utricularia*

Paramo Vegetation:

None

Coastal Dune Vegetation:

cf. *Acacia, Casearia, Coccoloba, Iresine, Laguncularia, Terminalia, Tournefortia*

Genera occurring in secondary vegetation:

Alibertia, Allophylus, Alnus, cf. *Acacia, Borreria, Buettneria, Combretum, Casearia, Cuphea, Cedrela, Desmanthus, Eugenia, Hibiscus, Iresine, Mimosa, Passiflora, Securidaca, Serjania, Smilax, Tournefortia*

Since the common plants of Paramo vegetation belong to stenopalynous groups, and grow removed from the depositional basin, it is not possible to assess the presence of this community on palynological evidence. As noted earlier, however, there is no reason to assume the absence of the Paramo during the upper Miocene since highlands have been available in eastern Mexico since post-Cretaceous times.

Pollen of *Abies* in the Paraje Solo microflora documents the presence of the Needle-Leaved Forest among Miocene communities of Veracruz. Pollen of *Pinus* and *Quercus* is also represented, and these are dominant elements of the pine and pine-oak forests characteristic of high elevations in Mexico. In addition to the dominants, pollen of wider-ranging genera frequently associated with the Needle-Leaved Forest was recovered including *Smilax, Alchornea*, cf. *Sapium, Coccoloba*, and *Alnus*. The genus *Stillingia* is not presently known from Veracruz, but elsewhere it is associated with pine-oak forests. Several grains of *Picea* were found in 5 samples distributed among 3 sites (Table 1). Thus spruce was a significant member of the coniferous forest of Veracruz during the upper Miocene. The genus no longer occurs in Veracruz, and is represented in Mexico today only by *P. mexicana* Martínez (Coahuila, Nuevo León) and *P. chihuahuana* Martínez (Chihuahua, Durango; Gordon, 1968). The dominant member of the Scale-Leaved Forest, *Juniperus deppeana* Steud., and the commonly associated *Nolina* and *Sophora*, have not been identified in the microflora. Thus among the Needle-Leaved Forests there is evidence for the cool moist Bosque de Oyamel (*Abies, Picea*), Bosque de Pino (*Pinus*), and Bosque de Pino-Encino (*Pinus, Quercus*), but little evidence of the drier and warmer Bosque de Cedro y Tásate (*Juniperus, Nolina, Sophora*).

The Broad-Leaved Forests are oak communities of high elevations (evergreen oak), moderate elevations (temperate oak), and low elevations (warm oak). Each community is characterized by particular species of *Quercus* and associated genera. Since these species of oak cannot be distinguished on the basis of pollen characters, it is not possible to record precisely the type of Broad-

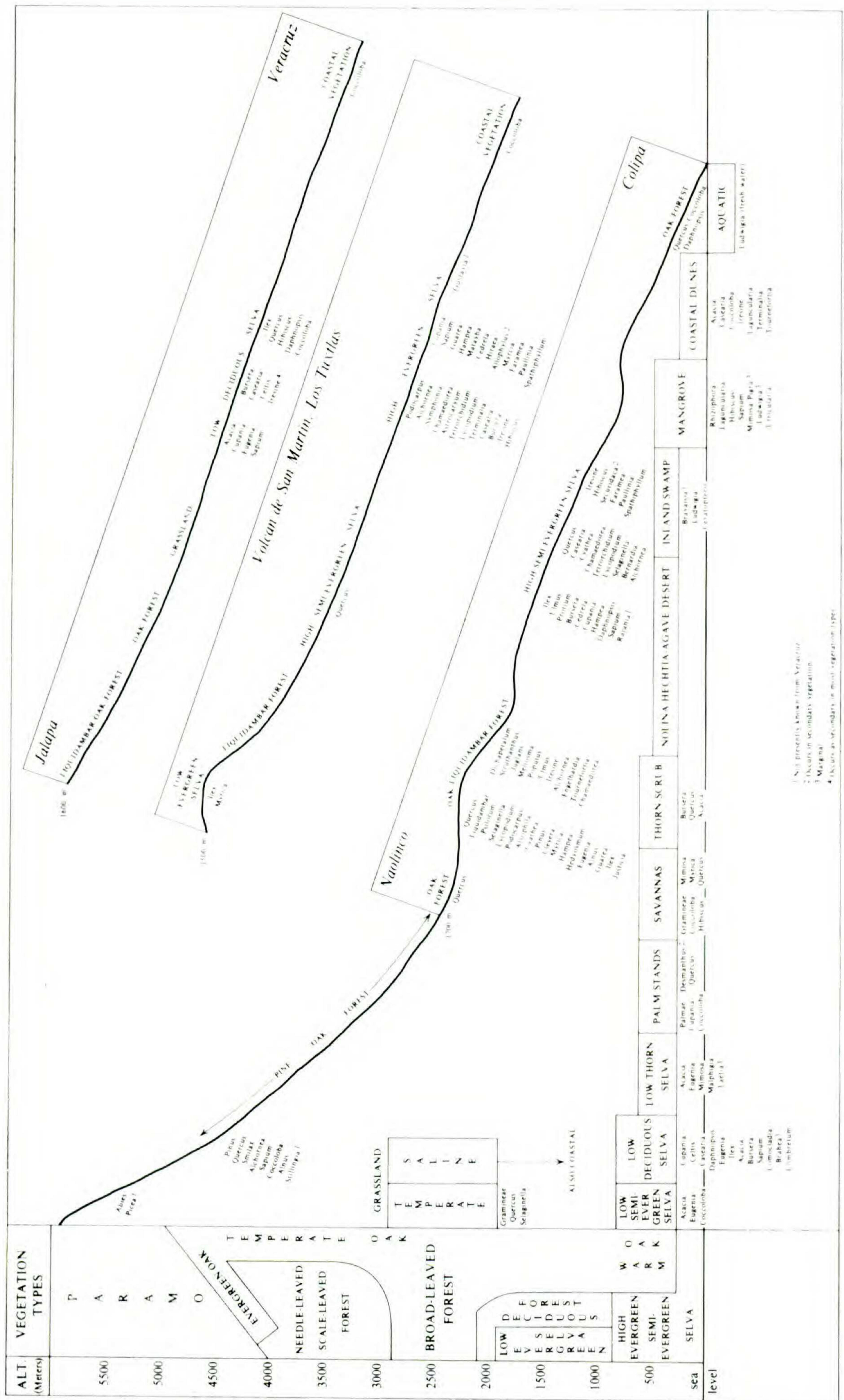
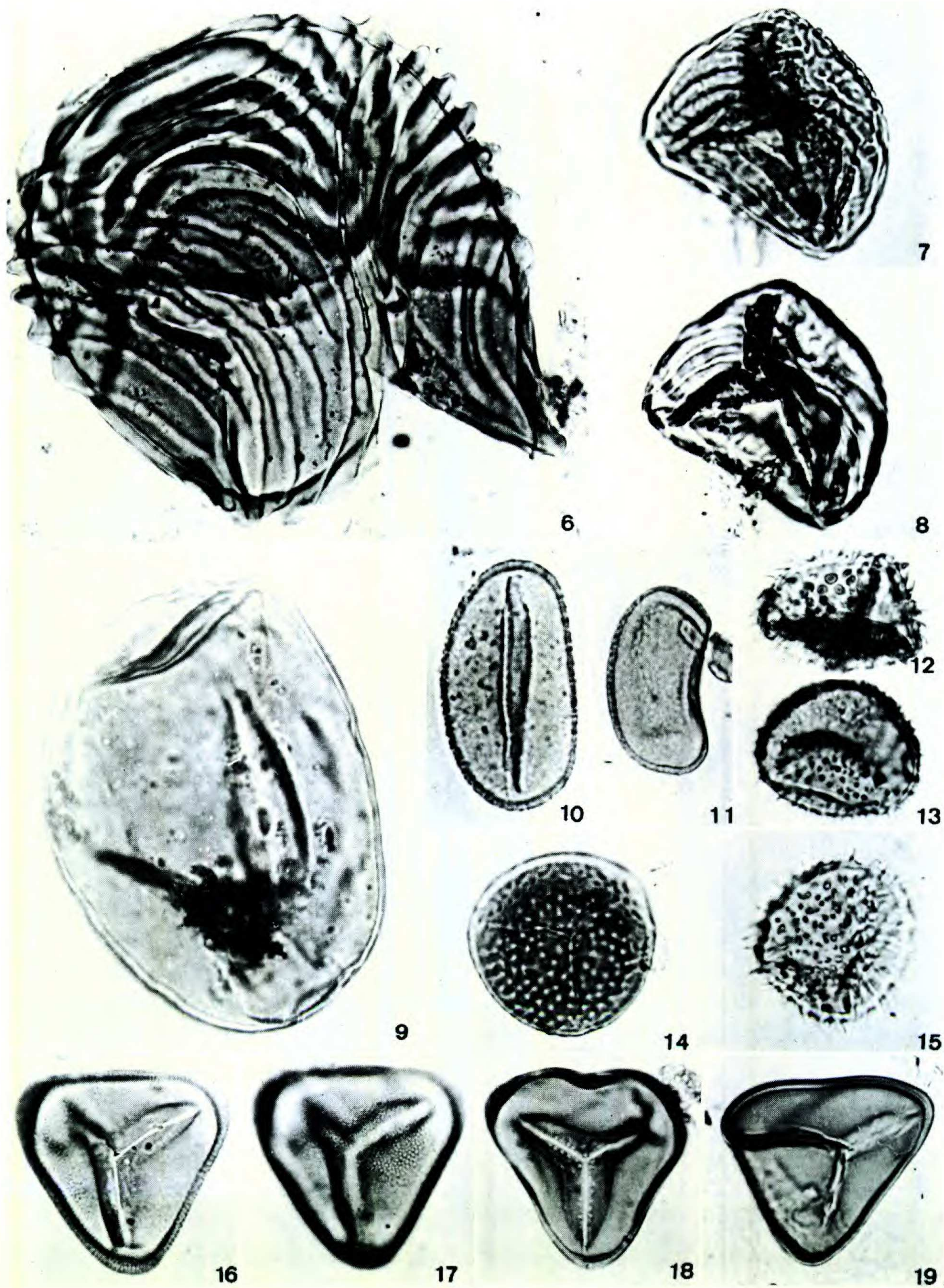
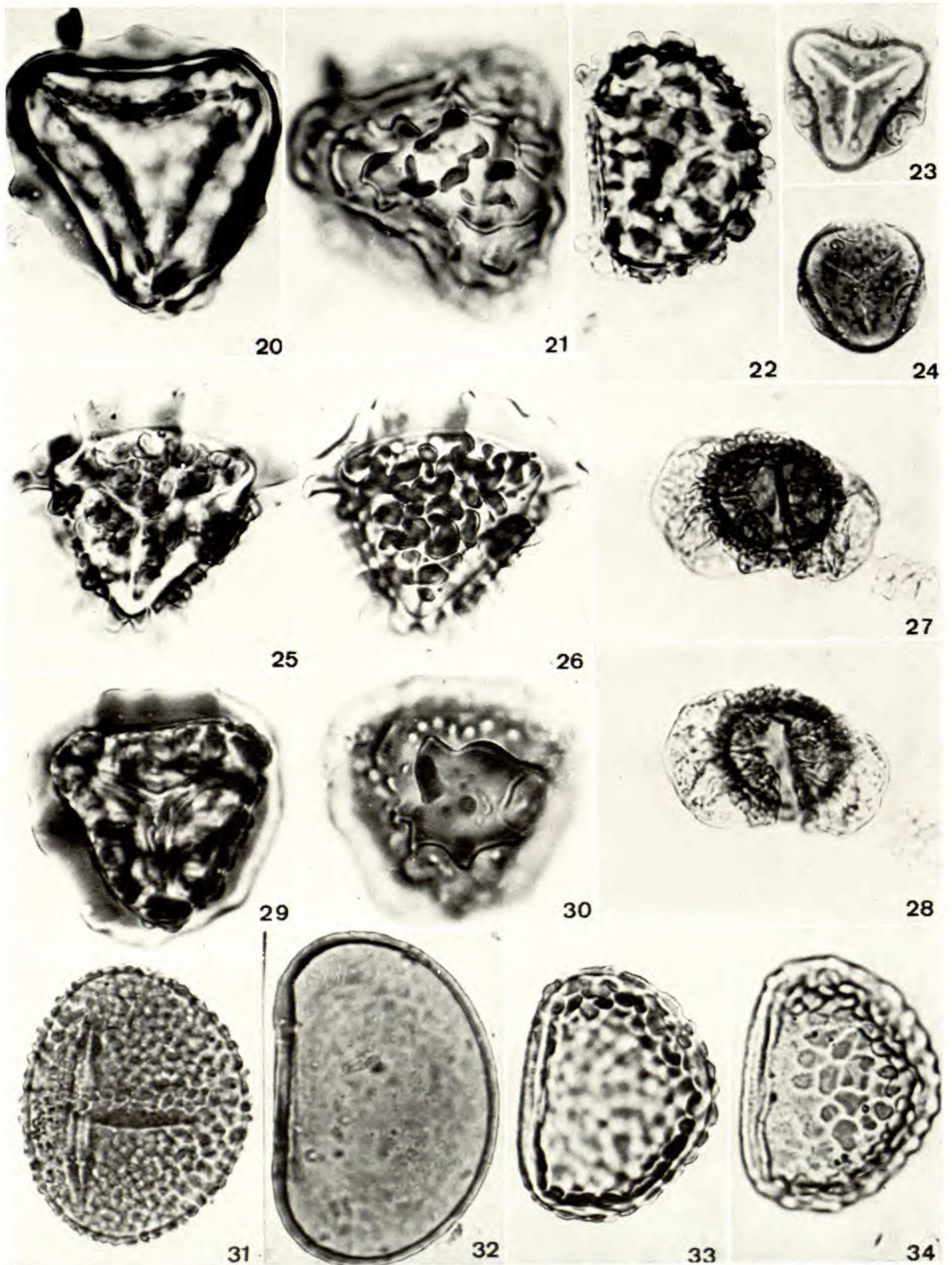


FIGURE 5. Taxa of plant microfossils arranged according to present-day communities. See text for further explanation.



FIGURES 6-19.—6. *Ceratopteris*, 44-1, V-30, 125 μ .—7-8. *Pityrogramma*, 5-1, C-12, 45 μ .—9. *Lomariopsis* (*Stenochlaena*), 8-1, U-32, 72 \times 52 μ .—10. *Dicranopteris*, 19-1, E-11,1, 50 \times 29 μ .—11. *Psilotum*, 37-1, K-12,2-4, 36 \times 18 μ .—12-13, 15. *Selaginella*.—12. 10-1, Q-39,1, 36 μ .—13. 40-1, N-21,1-3, 32 μ .—15. 10-1, B-44,1, 38 μ .—14. *Lycopodium*, 38-1, P-18,1-3, 37 μ .—16-18. *Alsophila*.—16-17. 2-1, S-30, 50 μ .—18. 34-1, O-14,1, 41 μ .—19. *Cyathea*, 13-1, T-36,2, 41 μ . [The numbers following plant names represent sample and slide number (e.g., 44-1), England Slide Finder coordinates (e.g., V-30), and size (e.g., 125 μ).]



FIGURES 20-34.—20-21, 25-26, 29-30. *Pteris*.—20-21. Type 1, 10-1, Q-25,3, 63 μ .—25-26. Type 2, 13-1, N-41,1, 59 μ .—29-30. Type 3, 25-1, D-29, 54 μ .—22, 31-34. Polypodiaceae.—22. Type 4, 30-1, V-26,1, 49 \times 39 μ .—31. Type 3, 25-1, K-48,2-4, 56 \times 48 μ .—32. Type 1, 32-1, X-42,2, 69 μ .—33-34. Type 2, 13-1, R-22,4, 54 \times 41 μ .—23-24. *Hemitelia*. 23. Type 1, 35-1, Q-48,2, 32 μ .—24. Type 2, 1-1, M-48, 37 μ .—27-28. *Podocarpus*. 25-1, R-41,3, 31 \times 22 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

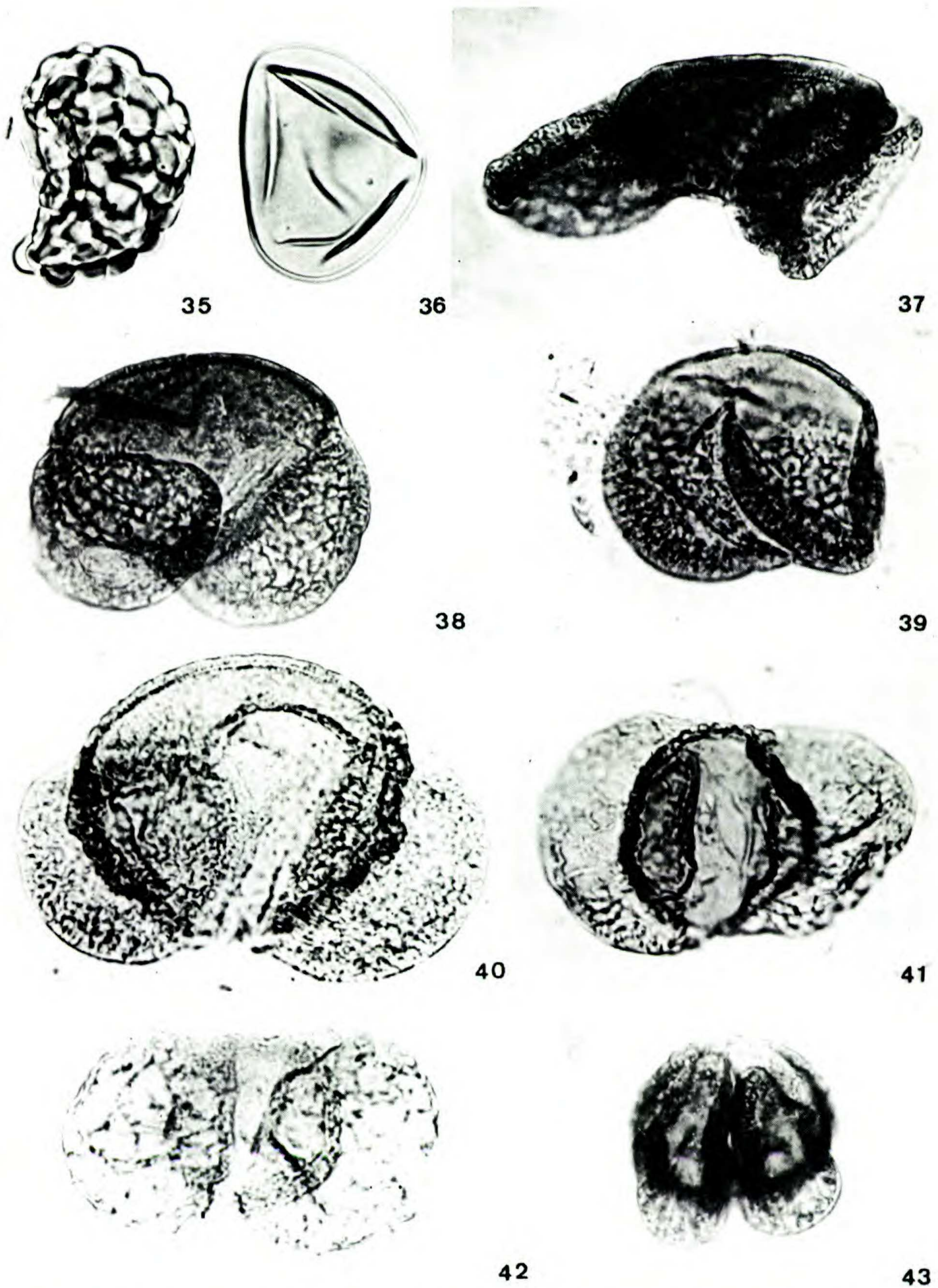
TABLE 4. Synopsis of genera and distributional ranges of taxa represented by fossil pollen and spores in the Paraje Solo Formation, but presently unreported for the modern flora of Veracruz. Tentative identifications (e.g., cf. *Brahea*) are not included. *Symphonia*, unverified for the modern flora at the beginning of the study, has recently been reported from the High Evergreen Selva (Gómez-Pompa, pers. comm., 1974).

<i>Ceratopteris</i>	A floating fern of Tabasco, Central America (Guatemala, Honduras, El Salvador, Costa Rica, Panama), and the Greater Antilles (Cuba, Haiti, Dominican Republic, Puerto Rico).
<i>Picea</i>	Highlands of northern Mexico; <i>P. chihuahuana</i> (Chihuahua, Durango) and <i>P. mexicana</i> (Coahuila, Nuevo León).
<i>Gustavia</i>	Costa Rica, Panama, and south (Colombia, Venezuela, the Guianas, Brazil, Peru).
<i>Laetia</i>	Campeche, Tabasco, Yucatán, Chiapas, Quintana Roo, Central America (British Honduras, Guatemala, Panama), and the Antilles (Cuba, Andros in the Bahamas, Dominican Republic, Jamaica, Martinique).
<i>Rajania</i>	A West Indian segregate of <i>Dioscorea</i> ; Cuba, Hispaniola, Jamaica, Puerto Rico.

Leaved Forest present in Veracruz during the Miocene. Fossil pollen of *Quercus* is present at all sites, however, and at site 6 reaches 34% of the microflora. Since no members of the high (e.g., *Abies*, *Picea*, *Pinus*) or middle (e.g., *Liquidambar*) altitude communities reach such high percentages, it is likely that site 6 records the presence of a lowland oak assemblage, possibly of *Q. oleoides* Cham. & Schlecht.

The Deciduous Forest south of Misantla consists of *Liquidambar macrophylla* Oerst. and several species of oak, including *Q. affinis* Schwidw. as dominants. In the Sierra de Los Tuxtlas the dominants are *L. macrophylla*, *Q. skinneri* Benth., *Ulmus mexicana* Liebm., and *Meliosma alba* (Schlecht.) Walp. (Sousa, 1968). Pollen of all these genera occur in the Paraje Solo Formation. In addition, pollen of a number of genera commonly associated with the oak-*Liquidambar* forest are also present (Fig. 5). The Deciduous Forest is one of the principal associations represented in the microflora, in contrast to the selvas, remnants of which presently occupy much of the Veracruz lowland.

Selvas are not well represented in the Paraje Solo microflora considering the diversity of genera and lowland habitat of these communities. The High Evergreen Selva of Veracruz includes *Terminalia amazonica* (Gmel.) Exell, *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Swartz, *Ficus tecolutensis* (Liebm.) Miq., and *Pseudolmedia oxyphyllaria* Donnell Smith as frequent multi-dominants. Among these *Terminalia* pollen is tentatively recorded, but these grains are similar to *Combretum*. One species (*T. catappa* L.) grows outside the selvas in Coastal Dune and Island Vegetation (Gómez-Pompa, 1973: 139-143), but it is considered introduced. Common associates of the High Evergreen Selva recorded in the microflora are frequently genera found in other communities, such as *Podocarpus* and *Guarea* in the Deciduous Forest, species of *Bursera* in the Thorn Scrub and Low Deciduous Selva, and *Alchornea* and cf. *Sapium* widespread through several associations. A few genera most commonly found



FIGURES 35-43.—35-36. Polypodiaceae.—35. Type 5, 10-1, 0-41,3, $53 \times 36 \mu$.—36. Type 6, 13-1, X-36,3, $47 \times 36 \mu$.—37. *Abies*, 2-1, E-20,2-4, $110 \times 40 \mu$.—38-39. *Picea*.—38. 5-1, L-42,1-3, $72 \times 50 \mu$.—39. 37-1, B-24,1, $63 \times 45 \mu$.—40, 43. *Pinus*.—40. Type 1, 21-1, L-16, $98 \times 60 \mu$.—43. Type 2, 4-1, P-35,1, $45 \times 36 \mu$.—41-42. *Podocarpus*.—41. 40-1, P-17,1, $72 \times 47 \mu$.—42. 9-1, S-48,2, $76 \times 47 \mu$. [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

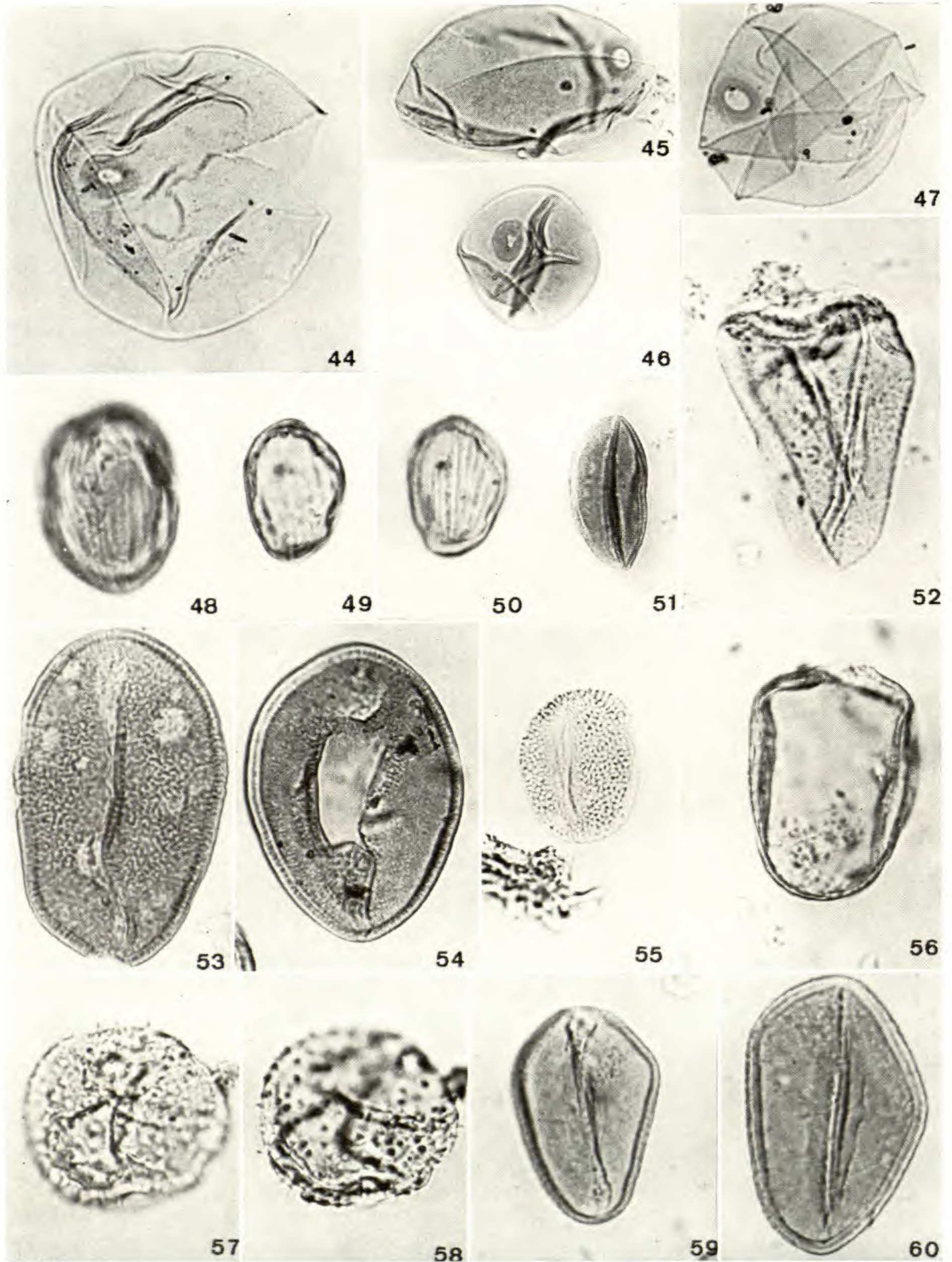
in the High Evergreen Selva are present in the microflora (e.g., *Hiraea*, *Myrcia*). However, considering the near absence of the dominants and infrequent occurrence of equivocal associates, the High Evergreen Selva appears to have been less well-defined and of more restricted distribution during the upper Miocene than at present. The same is true for the related High Semi-Evergreen and Medium Semi-Evergreen selvas (Fig. 5).

The remainder of the selvas grow in environments of reduced rainfall (e.g., to the lee of local highlands) or under edaphic conditions (poor, coarse soil) resulting in moisture stress. This category of drier to arid communities is poorly represented in the Paraje Solo microflora. Among genera found in the Low Evergreen Selva only the wide-ranging *Ilex* and *Myrica* were recovered. None of the characteristic genera of the Low Semi-Evergreen Selva are presently known from the fossil assemblage, with the possible exception of *Coccoloba* which is found in other types of vegetation. None of the dominants of the Low Deciduous Selva have been found, but this community is represented by some common associates (cf. *Acacia*, cf. *Brahea*, *Bursera*, *Casearia*, *Celtis*, *Combretum*, *Comocladia*, *Cupania*, *Daphnopsis*, *Eugenia*, *Ilex*, and cf. *Sapium*). Similarly the Low Thorn Selva is represented by cf. *Acacia*, *Eugenia*, cf. *Malpighia*, *Mimosa*, and *Laetia* (presently unknown from Veracruz; Table 4). Some of these range into more mesic communities (e.g., *Eugenia* in the Deciduous Forest), and it is probably significant that the fossil pollen of cf. *Acacia* appears most similar to *A. farnesiana* (L.) Willd. and *Mimosa* to *M. pigra* L. These two species have relatively broad ecological tolerances and extend into more humid environments than is usual for the respective genera.

Progressing to more xeric and distinctly arid vegetation types, not only the dominants but almost all important associated genera are absent from the Paraje Solo microflora. This includes the *Nolina-Hechtia-Agave* Desert and the Thorn Scrub. Among genera listed for the former by Gómez-Pompa (1973: 135–137) none are represented, and from the latter, pollen of only *Bursera*, cf. *Acacia* and *Quercus* is present. Although individual elements of a subhumid vegetation are represented in the fossil assemblage, there is little evidence they were aggregated into definite communities of wide distribution in southeastern Veracruz.

The occurrence of two communities in Veracruz, the Palm Stands and Savannas, are of interest because of possible anthropogenic influences necessary for their genesis and persistence. Three genera of palms occur as stands in Veracruz, *Scheelea*, *Sabal*, and *Paurotis*. Pollen of these has not been recovered, and the amounts of six other palm types do not suggest stands of palms (Table 1), but rather scattered occurrence as elements in other vegetation types. Although these results are not directly related to the problem of origin of palm stands in Veracruz, it is likely, considering the lowland distribution of the plants, that *Scheelea*, *Sabal*, and *Paurotis* stands are at least of post upper Miocene development in south coastal Veracruz.

The problem of savannas is more difficult. The various genera of grasses, occurring in almost all kinds of communities, cannot be distinguished in the microflora. Also the number of nongrass genera consistently associated with the savanna in Veracruz (e.g., *Curatella americana* L.) is few, and therefore



FIGURES 44-60.—44-47. Gramineae.—44. 10-1, W-41,3, 63 μ .—45. 2-1, Y-45,1, 50 μ .—46. 2-1, R-30,1, 36 μ .—47. 13-1, Y-12,2, 50 μ .—48-50. *Spathiphyllum*.—48. 8-1, P-49, 35 \times 22 μ .—49-50. 34-1, Q-36,3, 29 \times 20 μ .—51. Cf. *Brahea*, 1-1, G-22,4, 40 \times 20 μ .—52, 56. Cyperaceae.—52. 21-1, S-46, 58 μ .—56. 30-1, P-32,2, 49 μ .—53. Cf. *Astrocaryum*, 40-1, L-10,2, 68 \times 44 μ .—54. Cf. *Maximiliana*, 2-1, K-29, 60 \times 45 μ .—55. Cf. *Chamaedorea*, 4-1, D-31,4, 32 \times 23 μ .—57-58. *Smilax*, 4-1, W-34,4, 41 μ .—59-60. Cf. *Attalea*.—59. 45-1, X-43,4, 45 \times 32 μ .—60. 45-1, Q-11,1-2, 54 \times 36 μ . [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

absence of this pollen in the microflora may not be significant. Considering savanna plants from Veracruz (Gómez-Pompa, 1973: 128–132) and Chiapas (Breedlove, 1973: 159–160) only *Hibiscus*, *Mimosa*, and *Myrica*, together with the grasses, possibly reflect the presence of savannas, and these genera are not diagnostic for the savannas. On the basis of limited evidence it appears more likely that Temperate and Saline grasslands account for the high percentage of grass pollen (maximum 45%) at site 4 (Table 1).

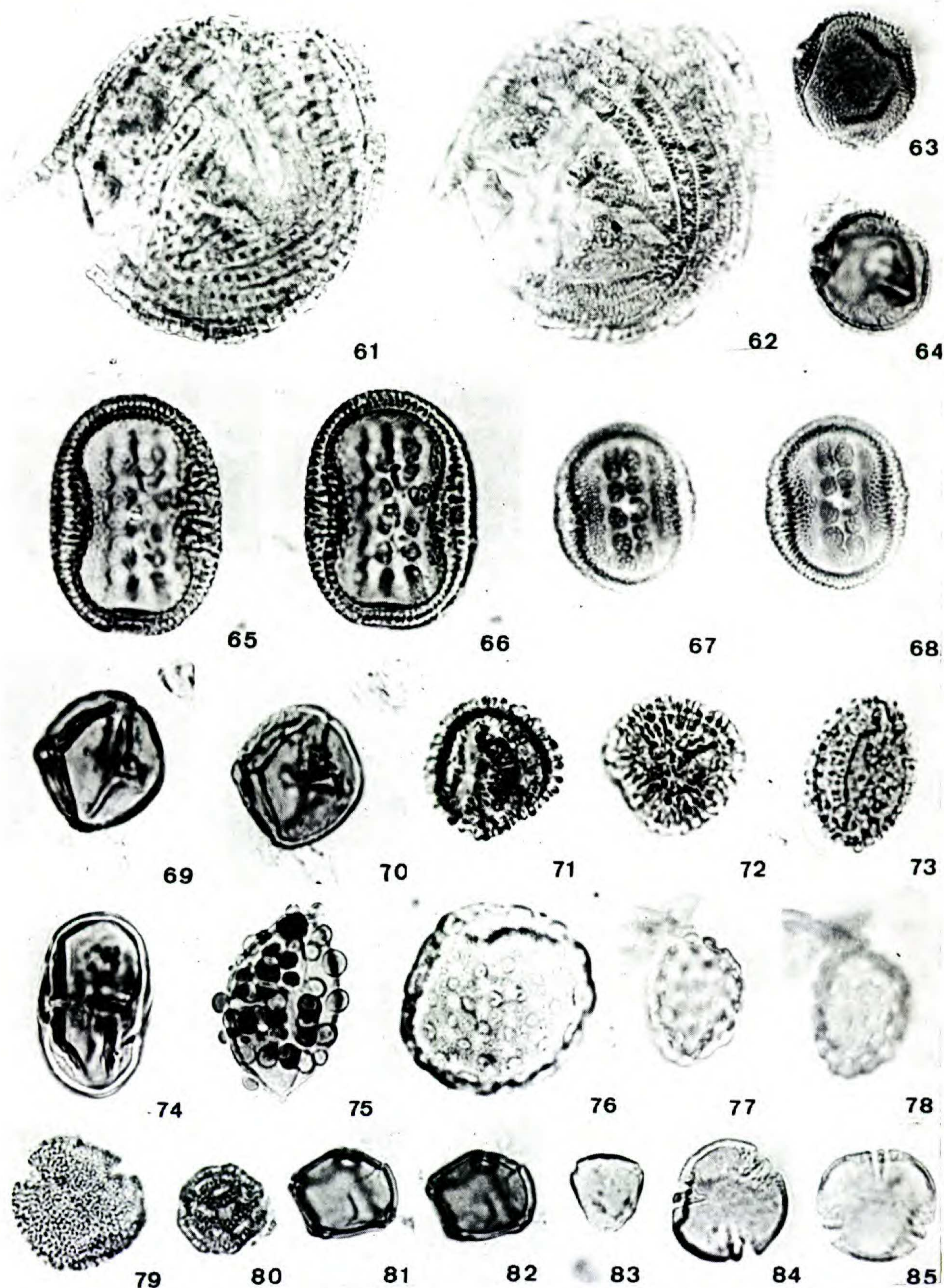
The most common pollen type in the Paraje Solo microflora is *Rhizophora* (maximum 96%, site 5). This is the dominant genus along the outer fringes of modern Manglar vegetation, with *Avicennia*, *Conocarpus*, and *Laguncularia* growing further inland. Pollen of *Laguncularia* is also abundant in the Paraje Solo Formation, especially at sites 3, 4, and 5. Elements from related swamp vegetation dominated by *Pachira aquatica* Aubl., found in waters of very slight salinity, also are present in the fossil assemblage. These include *Hibiscus*, *Laguncularia*, *Rhizophora*, and cf. *Sapium*. The large amounts of *Rhizophora* and *Laguncularia* pollen, with several associated genera, document Manglar as an important community in the upper Miocene vegetation of southern Veracruz.

Sedge pollen is found in the microflora in small amounts. The grains are thin-walled and frequently folded. Since the wedge shape is a characteristic feature of sedge pollen, percentages reported are usually minimum values. The Inland Swamps of Veracruz are characterized by the Cyperaceae together with other plants such as *Thalia geniculata* L. and *Pontederia sagittata* Presl. Fossil pollen of *Thalia* and *Pontederia* has not been found and direct evidence for the presence of Inland Swamps is equivocal, but there is little reason to assume the absence of this community within a documented lowland environment.

Evidence for Coastal Dune vegetation near Coatzacoalcos during the upper Miocene is substantial. Pollen of cf. *Acacia*, *Casearia*, *Coccoloba*, *Iresine*, *Laguncularia*, *Terminalia*, *Tournefortia*, and numerous composites, grasses, and chenopods is common and all are members of this community (Gómez-Pompa, 1973: 139–143). For reasons to be considered in the discussion on paleoenvironments, it is likely that elements present in the microflora reflecting subhumid environments belong to the edaphically dry Coastal Dunes and Island Vegetation, and possibly to a Low Deciduous Selva type community occupying areas of physiographically controlled reduced rainfall (e.g., to the lee of the Sierra de Los Tuxtlas). There is little evidence of extensive climatically dry selvas, Thorn Scrub, and Deserts.

Pollen of Aquatic Vegetation has not been identified in the microflora, but for reasons noted earlier, this community is frequently underrepresented in lignites. Aquatic Vegetation is often of scattered and restricted distribution, pollen production is low, exines are occasionally poorly developed, and many belong to stenopalynous Gramineae, Cyperaceae, and Compositae (as marginal fringe vegetation). As with the Paramo and Inland Swamps, there is no climatic, physiographic, or stratigraphic (age) evidence suggesting these communities would be inappropriate to the upper Miocene landscape of Veracruz.

In summary, several communities of the modern flora of Veracruz are evident in the upper Miocene by pollen of characteristic dominant and associated



FIGURES 61-85.—61-62. *Bravaisia*, 34-1, 0-33,2, 58 μ .—63-64. *Bursera*.—63. 2-1, K-18,4, 34 μ .—64. 40-1, U-12, 26 μ .—65-68. *Justicia*.—65-66. 30-1, L-21,1, 56 \times 36 μ .—67-68. 2-1, E-16,1, 45 \times 36 μ .—69-70. *Comocladia*, 35-1, R-30,2, 28 μ .—71-73. *Ilex*.—71-72. 10-1, E-14,2-4, 33 μ .—73. 35-1, R-17,1, 45 \times 32 μ .—74. *Protium*, 1-1, Y-23,1, 33 \times 21 μ .—75. *Tournefortia*, 13-1, W-20, 29 \times 31 μ .—76-78. *Amaranthaceae-Chenopodiaceae*.—76. 21-1, E-17, 41 μ .—77-78. 10-1, H-30,3-4, 26 μ .—79. *Hedyosum*, 13-1, R-47,2-4, 30 μ .—80. *Iresine*, 8-1, Y-23,1, 18 μ .—81-82. *Alnus*, 38-1, M-31, 23 μ .—83. *Dichapetalum*, 25-1, D-10,2-4, 15 μ .—84-85. *Alchornea*.—84. 10-1, T-18,1, 23 μ .—85. 9-1, G-41,2-4, 24 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

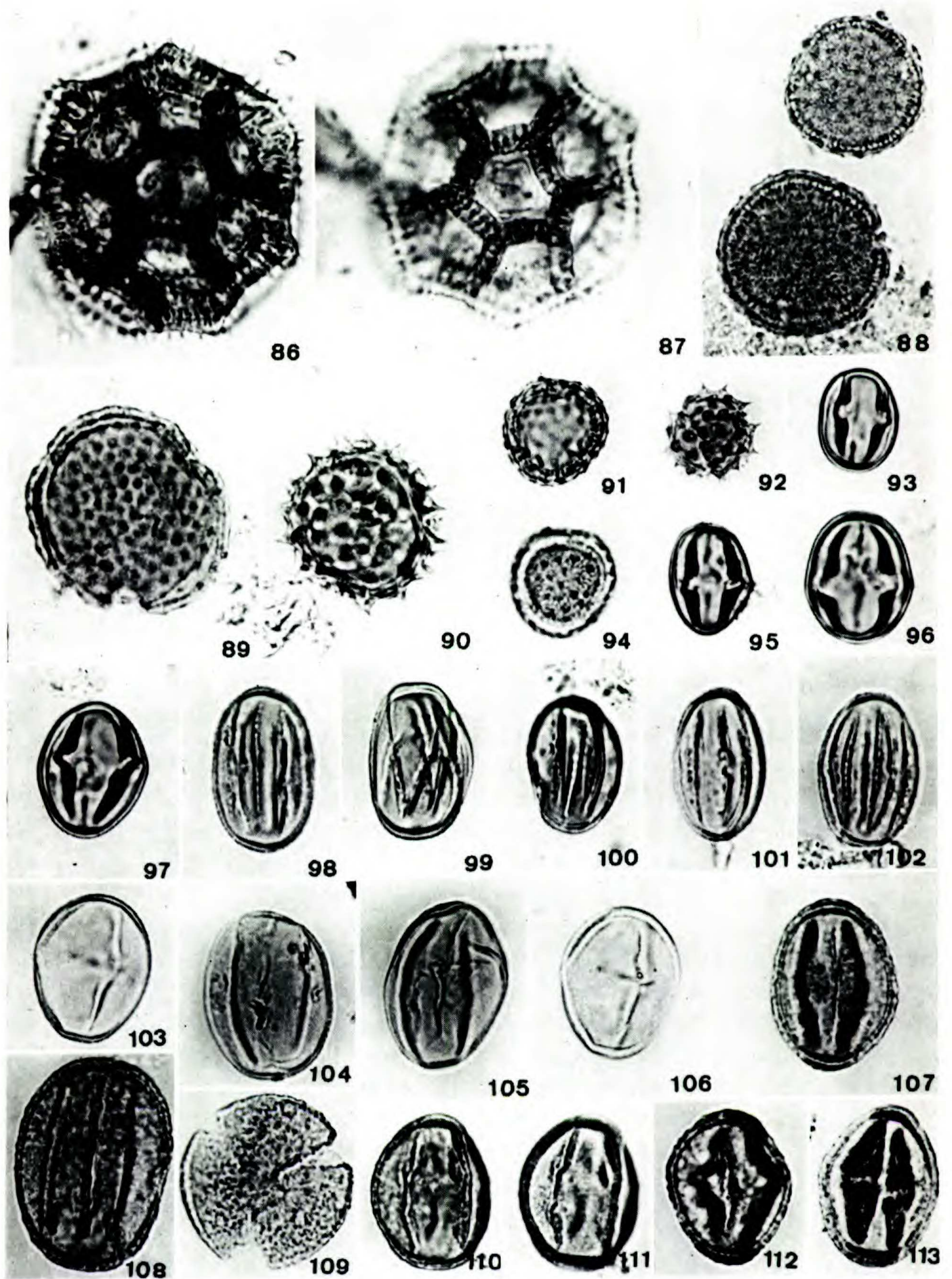
genera. These include the Needle-Leaved Forests of Bosque de Oyamel, Bosque de Pino, and Bosque de Pino-Encino; the Broad-Leaved Forests of warm, and probably temperate and evergreen oak communities; the Deciduous Forest; Temperate and Saline Grasslands; Mangrove Swamps; Coastal Dune Vegetation; and possibly a restricted and modified Low Deciduous Selva type of community. Some other types of vegetation, underrepresented for various reasons, were likely present. These are the Paramo, Inland Swamps, and Aquatic Vegetation. Absent or poorly represented vegetation types are the Scale-Leaved Forests (Bosque de Cedro y Tásate); High Evergreen Selva; High Semi-Evergreen Selva; Medium Semi-Evergreen Selva; Low Evergreen Selva; Low Semi-Evergreen Selva; Low Thorn Selva; Palm Stands; Savannas; *Nolina-Hechtia-Agave* Desert; and Thorn Scrub.

MEGAFOSSILS

Only a single paper describes a substantial megafossil flora from Tertiary deposits in Mexico (Berry, 1923). The specimens are from two presumed Miocene localities in southern Mexico. One is in the state of Oaxaca near Palomares, along Mexico 185 about mid-way between Matías Romero and the Oaxaca-Veracruz border. The flora consists of *Acrostichum mexicanum* Berry, *Gymnogramme wadii* Berry [*Gymnocladus wadii* (Berry) Maldonado-Koerdell, 1950], *Anacardites lanceolatus* Berry, *Anona saraviana* Berry, *Bignonioides orbicularis* Berry, *Connarus carmenensis* Berry, *Crescentia cucurbitinoides* Berry, *Dioclea?* *mexicana* Berry, *Drypetes elliptica* Berry, *Fagara wadii* Berry, *Ficus?* *talamancana* Berry, *Goepertia* cf. *G. tertiaria* Berry, *Gouania miocenica* Berry, *Guet-tarda cookei?* Berry, *Lecythidophyllum couratarioides* Berry, *Leguminosites oaxacensis* Berry, *Melastomites angustus* Berry, *M. obovatus* Berry, *Moquillea mexicana* Berry, *Myrcia saraviana* Berry, *Nectandra areolata* Engelhardt, *N. tehuantepecensis* Berry, and *Rondeletia?* sp.

The second locality is in the state of Veracruz near San José del Carmen, southeast of Coatzacoalcos. The village is an outlier of the larger adjacent settlement of Las Choapas about 25 km S of Mexico 180. The flora consists of *Gymnogramme wadii* Berry [*Gymnocladus wadii* (Berry) Maldonado-Koerdell, 1950], *Allamanda carmenensis* Berry, *Apocynophyllum mexicanum* Berry, *Cedrela miocenica* Berry, *Connarus carmenensis* Berry, *Coussapoa veracruziana* Berry, *Inga miocenica* Berry, *Leguminosites mexicanus* Berry, *Liquidambar incerta* Berry, *Melastomites obovatus* Berry, *Mespilodaphne palomarensis* Berry, and *Simaruba veracruziana* Berry.

Later, Mullerried (1938) described *Juglans veracruzana* from Tertiary deposits near Tlacolulan, just northwest of Jalapa, and Miranda (1963) recorded *Acacia* sp. and *Tapirira durhamii* Miranda from Oligo-Miocene ambers near Simojovel in the state of Chiapas. Breedlove (pers. comm., 1971) notes the presence of fragmentary plant remains in Chiapas, and in 1961 specimens of well-preserved angiosperm leaves were examined in the posada of Franz Blom, San Cristóbal. These had been collected by local inhabitants and the source was unknown. Considering the depositional environments along the eastern coastal plain of southern Mexico, it is likely that numerous fossil plant localities



FIGURES 86-113.—86-92, 94. Compositae.—86-87. Type 1, 19-1, T-30,1-3, 63 μ .—88. Type 2, 17-1, W-10, 34 μ .—89. Type 3, 10-1, V-41, 45 μ .—90. Type 4, 17-1, P-11,3, 37 μ .—91, 94. Type 5, 25-1, X-38,4, 21 μ .—92. Type 6, 2-1, U-38,1, 27 μ .—93, 95-97. *Laguncularia*.—93. 25-1, V-25,2, 22 \times 15 μ .—95. 33-1, K-32, 23 \times 16 μ .—96. 25-1, J-20,3, 27 \times 22 μ .—97. 30-1, W-31,3-4, 29 \times 22 μ .—98-102. *Combretum/Terminalia*.—98. 17-1, Q-47, 1-3, 32 \times 20 μ .—99. 17-1, N-16,1, 32 \times 20 μ .—100. 17-1, X-32,2-4, 27 \times 19 μ .—101. 17-1, W-17,3-4, 29 \times 18 μ .—102. 17-1, W-9,3, 29 \times 20 μ .—103-106. *Rajania*.—103,106. 4-1, 0-34,3-4, 30 \times 22 μ .—104. 2-1, W-42,3, 34 \times 25 μ .—105. 2-1, W-18, 35 \times 24 μ .—107-113.

occur scattered through Veracruz, Oaxaca, and Chiapas. Because of the inaccessibility of much of the country and the brief exposure of new sites from the surrounding vegetation, detailed and sustained studies of Tertiary megafossil floras will most efficiently be made by resident investigators.

None of the above floras have been revised since original publication. From the collective list only *Acacia*, *Cedrela*, *Juglans*, and *Liquidambar* are represented as pollen in the Paraje Solo microflora.

PALEOENVIRONMENTS

The physical environment of southeastern Veracruz has been relatively stable during middle and late Cenozoic times. Relative sea level was slightly higher as evidenced by mangrove-containing lignites of the Paraje Solo Formation 8–12 m above present shorelines. The principal volcanic activity was uplift of the Sierra de Los Tuxtlas (1,700 m) beginning in the Miocene and culminating in the Plio-Pleistocene. Although these events modified local landscapes, major features of the physical environment were defined at the end of the Cretaceous and during the early Tertiary.

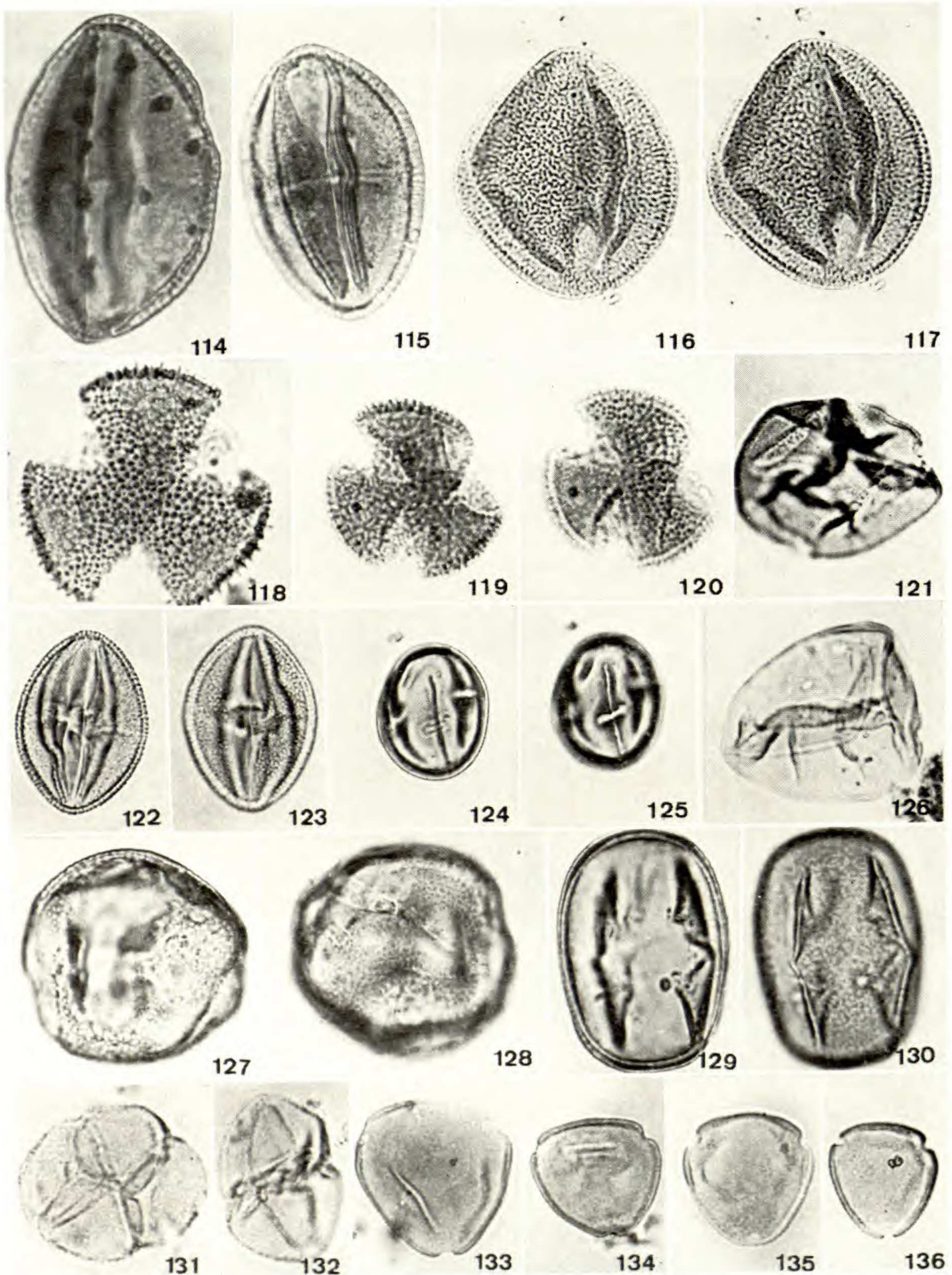
In the preceding discussion of Miocene communities certain differences were noted between the modern and ancient plant associations of southern Veracruz. These were: presence of a few genera now absent from Veracruz (notably *Picea*; Table 4), the expanded range of certain communities (Deciduous Forest), absence or poor representation of the Tropical Rain Forest, absence or poor representation of communities characteristic of dry to arid habitats, and absence or poor representation of vegetation types suspected, but not proven, to have originated, persisted and/or expanded under anthropogenic influence.

Several of these features of the paleocommunities can be attributed to slightly lower temperatures and possibly greater or more uniform distribution of rainfall during the upper Miocene than at present. The presence of well-preserved unfragmented pollen of *Picea*, a genus currently found only at high elevations (2,300–3,200 m; Gordon, 1968) over 1,000 km to the north (Chihuahua, Durango, Nuevo León), suggests cooler climates. A lowering of temperatures and increased or more uniformly distributed rainfall, however, in a floristically and topographically diverse region as Veracruz would have significant effect on several communities and these effects should be reflected in the composition of the fossil pollen flora.

One community particularly susceptible to lower temperatures would be the lowland Tropical Rain Forest, and this vegetation type is poorly represented in the Paraje Solo sediments. A comparison in Fig. 5 of the High Evergreen Selva (25 genera listed) with the oak-*Liquidambar* forest (29 genera) initially suggests comparable representation. However, for the oak-*Liquidambar* forest

←

Quercus.—107. 17-1, U-43,2-4, 35 × 24 μ.—108. 13-1, R-32,4, 41 × 31 μ.—109. 13-1, S-14,1, 37 μ.—110–111. 6-1, T-19,3-4, 32 × 24 μ.—112. 17-1, X-36,3, 32 × 26 μ.—113. 13-1, M-12,2, 35 × 27 μ. [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]



FIGURES 114-136.—114. Cf. *Stillingia*, 8-1, R-23, $54 \times 36 \mu$.—115. Cf. *Sapium*, 9-1, S-39,3, $58 \times 41 \mu$.—116-117. *Tithymalus*, 15-1, G-15,3-4, $50 \times 45 \mu$.—118-120. Cf. *Tetrorchidium*.—118. 54-1, T-44,1, 52μ .—119-120. 34-1, F-21,3, 36μ .—121. *Liquidambar*. 2-1, H-30,3-4, 38μ .—122-123. Cf. *Bernardia*, 10-1, B-13,3, $41 \times 28 \mu$.—124-125. *Casearia*, 6-1, V-18,3, $27 \times 22 \mu$.—126. *Juglans*, 54-1, Y-38,2-4, 36μ .—127-128. *Laetia*, 8-1, H-27, 49μ .—129-130. *Gustavia*, 25-1, 0-40, $52 \times 35 \mu$.—131-132. *Mimosa*.—131. 19-1, E-21,3-4, 27μ .—132. 19-1, U-14,4, $36 \times 25 \mu$.—133-136. *Engelhardtia*.—133. 2-1, U-28,1, 32μ .—134. 13-1, Q-37,2, 23μ .—135. 2-1, W-32, 27μ .—136. 2-1, U-35,3, 23μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

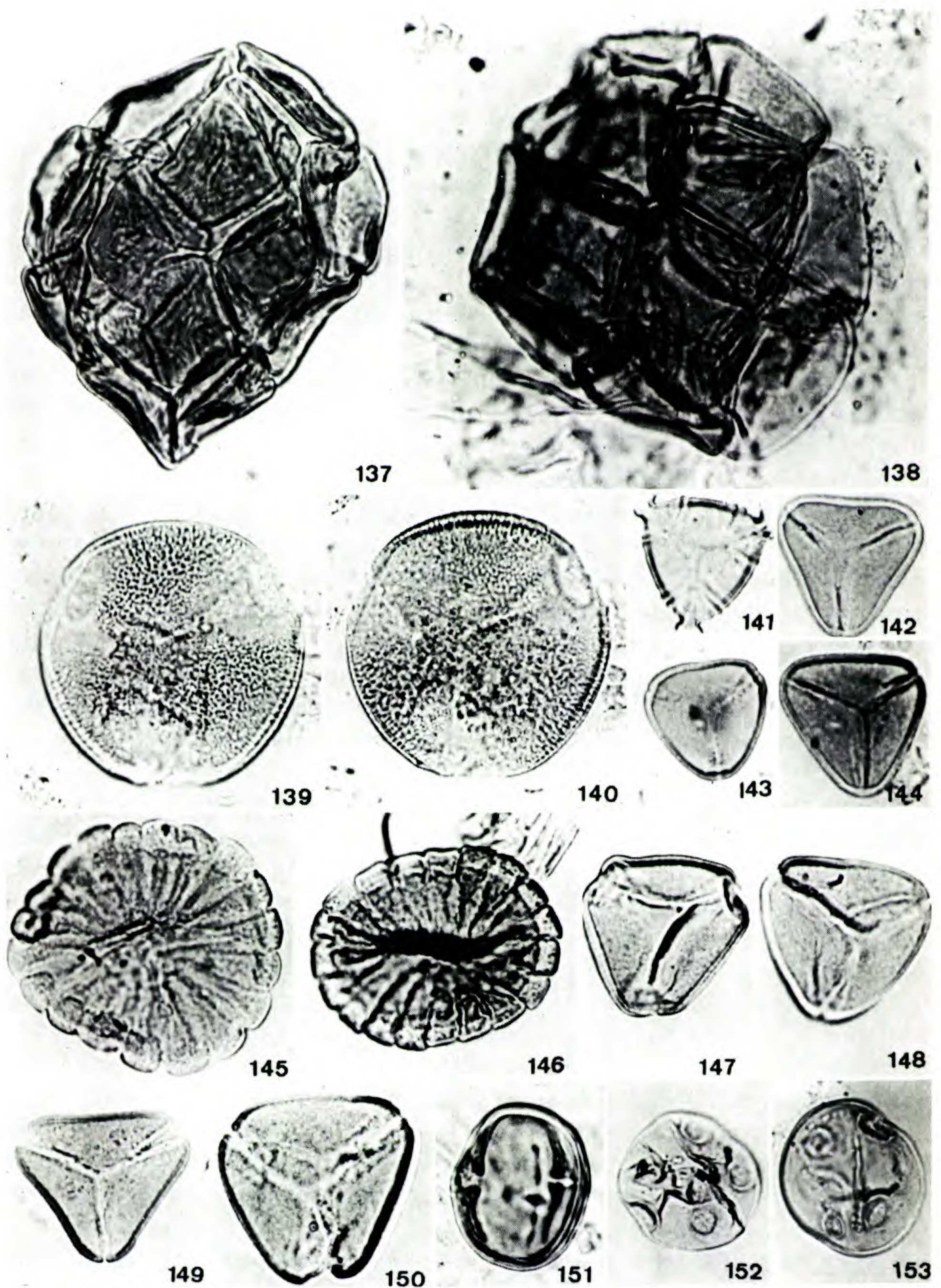
both dominants and a number of characteristically associated genera are present. Among the genera listed for the High Evergreen Selva, none of the dominants of the modern rain forest in Veracruz were recovered with the possible exception of *Terminalia amazonia* (J. F. Gmelin) Exell (identified as *Combretum/Terminalia*). Of the 25 genera present, 17 occur in other types of vegetation, one (*Allophylus*) occurs in secondary (disturbed) vegetation, one is a tentative identification (cf. *Hiraea*), and two have pollen similar to other nonrain forest genera (*Combretum/Terminalia*, *Eugenia/Myrcia*). Comparable results are being obtained by Palacios Chavez (unpublished data) for Tertiary deposits in Chiapas. In these sediments pollen of *Picea* was present and pollen of rain forest genera scarce or absent.

Regarding the absence of the dominant defining elements of the modern Veracruz rain forest in the Paraje Solo microflora, it is unlikely that this can be attributed entirely to low pollen production associated with entomophily. Although pollen of *Ficus tecolutensis* (Liebm.) Miq. would not be expected, the insect pollination of others is not so strict as to preclude entry of pollen into the sedimentary record (i.e., *Calophyllum brasiliense* Camb., *Dialium guianense* (Aubl.) Sandwith, *Bernoullia flammea* Oliver, *Brosimum alicastrum* Swartz, *Pseudolmedia oxyphyllaria* Donnell Smith; Rzedowski, pers. comm., 1974; Baker, pers. comm., 1975). Further, it is a characteristic of Tertiary microfloras from tropical regions that they contain pollen of entomophilous species (e.g., *Hibiscus*-type, Figs. 154, 156). This is probably due to "outwashing" of pollen under high rainfall regimes, particularly from lowland communities bordering basins of deposition (Germeraad et al., 1968: 206).

Within the complex mosaic of vegetation occupying the lowlands and adjacent slopes in Veracruz, there are diverse ecotypes capable of aggregating into various kinds of communities depending on the existing set of environmental conditions. Sarukhán (pers. comm., 1974) has suggested that if the Tropical Rain Forest were disrupted by slightly lower temperatures, expansion of the warm oak community of *Quercus oleoides* Cham. & Schlecht. would likely be favored. This suggestion is of interest because in these sediments where evidence for Tropical Rain Forest is meager, pollen of *Quercus* reaches 34% at site 6 (Table 1), far greater than would be expected from upland oak communities (Bosque de Pino y Encino; temperate and evergreen oak forests).

Gómez-Pompa (1973: 110), discussing a species list from the High Evergreen Selva, comments that: "Three species on this list that need further discussion are *Podocarpus guatemalensis*, *Quercus oleoides*, and *Sphaeropteris myosuroides*. They seem to be out of place in this type because, with the exception of *Sphaeropteris*, they have not been found growing in these selvas in any other areas in Veracruz, or even in Mexico. I cannot find any environmental explanation for this coincidence. The only possible explanation is that they are relicts of the old community that seems to have grown in these areas in the recent geological past when the area was cooler." The genus *Myrica* has also been found recently in the Veracruz lowlands, disjunct from its more common occurrence in the temperate upland Deciduous Forest.

Another relevant aspect of the microflora is the apparent lowering of eco-



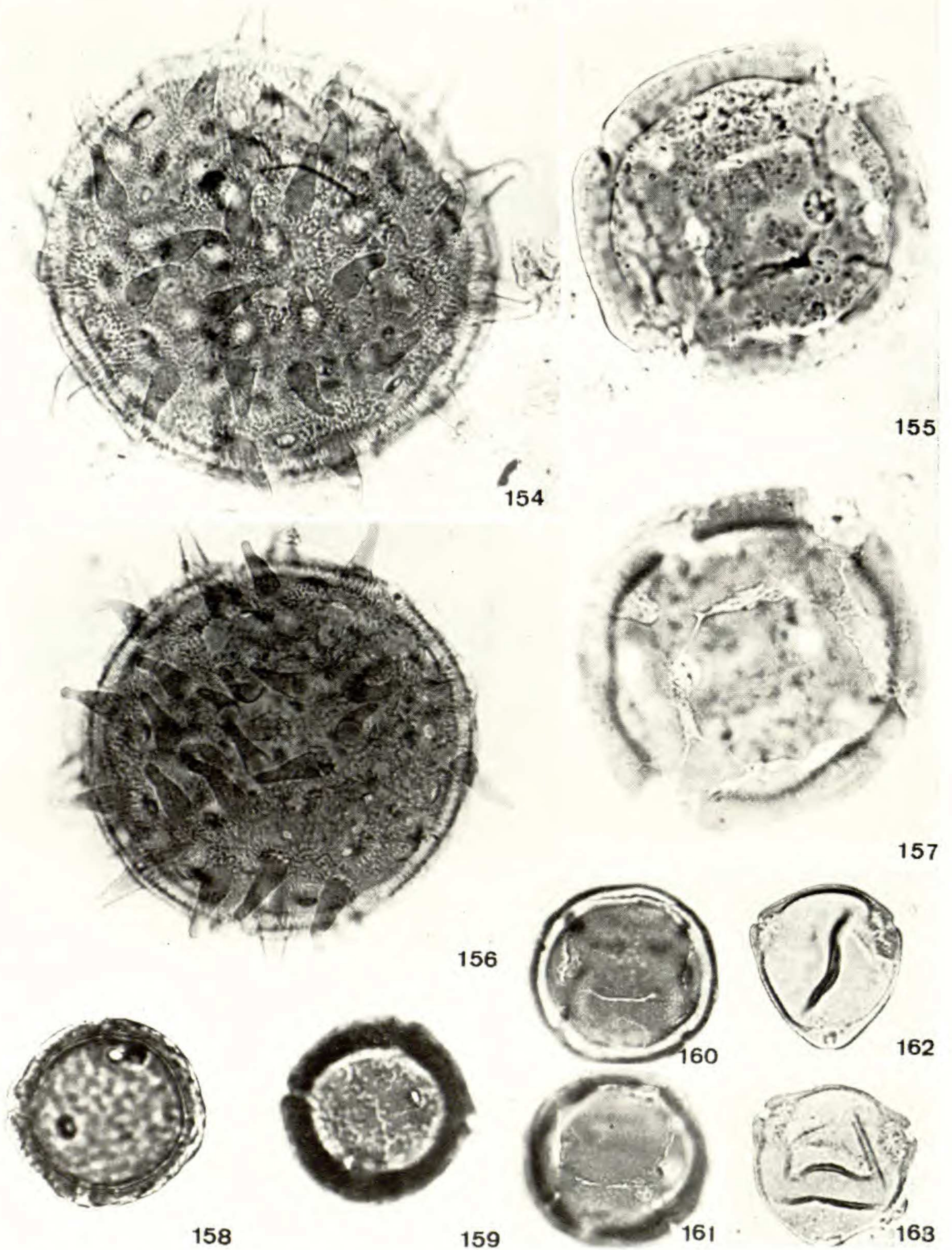
FIGURES 137-153.—137-138. Cf. *Acacia*.—137. 13-1, Q-15,4, $87 \times 72 \mu$.—138. 44-1, T-37,1-3, 85μ .—139-140. *Desmanthus*, 15-1, W-21,2-4, 58μ .—141. *Cuphea*, 25-1, V-49,4, 31μ .—142-144, 147-150. *Struthanthus*.—142. 49-1, K-26,2, 36μ .—143. 38-1, K-32,2, 24μ .—144. 32-1, X-42, 31μ .—147. 4-1, E-41,2, 30μ .—148. 4-1, R-40,1, 32μ .—149. 17-1, E-18,3, 30μ .—150. 4-1, C-28,4, 36μ .—145-146. *Utricularia*.—145. 19-1, J-46,3, 54μ .—146. 33-1, L-30,2, 49μ .—151. *Cedrela*, 10-1, S-9, $40 \times 31 \mu$.—152-153. *Guarea*.—152. 13-1, S-25,1, 30μ .—153. 6-1, W-19,1-3, 32μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

tones, bringing the Needle-Leaved Forest (*Abies*) and especially the Deciduous Forest into closer proximity to the depositional basin. The presence of these communities, well represented in the microflora, can most easily be explained by an extension of the Deciduous Forest ecotone below its present limit of about 1,000 m.

The introduction of temperate trees and shrubs disjunct from the deciduous forest of the eastern United States has been considered earlier (Graham, 1972, 1973). The opportunity for migration of some of these elements from north to south is based on late Tertiary climatic trends toward cooler conditions, and their early record in Eocene deposits of the Mississippi Embayment (Gray, 1960) with progressively later occurrences of a diminishing number of genera to the south. Approximately 60 species of arborescent plants are common to the temperate forests of the eastern United States and eastern Mexico (Graham, 1973: table 1). Estimates of the principal time of introduction of these plants into Mexico (Cretaceous to Pleistocene) includes virtually the entire geologic range of the angiosperms, primarily because adequate paleobotanical data was not available for eastern Mexico. The most commonly cited time of introduction is the Pleistocene (Deevey, 1949), when presumably elements of the eastern deciduous forest were forced into southern refugia during times of maximum glaciation. Although this is possible, data from the Paraje Solo assemblage in Veracruz document that some elements were already established in southeastern Mexico by late Miocene times. The earliest time of introduction is not known, but pollen of these temperate plants was not recovered from the Oligo-Miocene Simojovel Group of Chiapas (Langenheim et al., 1967). The late Miocene is an appropriate time for the range of some elements of the deciduous forest to expand into southern Mexico since world climatic models document that the climatic cooling, ultimately culminating in the Pleistocene glaciations, was already evident by the end of the Miocene (see summaries in Flint, 1971; Garner, 1974). Considering the number of taxa involved, however, (ca. 60 species of trees and shrubs plus herbaceous plants) it is probably that factors other than progressive introduction are involved in the complex relationships that exist between the eastern United States and eastern Mexico.

Axelrod (1975) has suggested a further explanation for these "Appalachian" disjuncts in the Mexican cloud forest. Rather than migrants from the north, he considers the modern vegetation along mid-altitude portions of the eastern Mexican Plateau as remnants of a "temperate rainforest" that during the early Tertiary (Eocene) extended in modified form into the Appalachian and other regions of the United States. As a result of later Cenozoic cooling climates, the evergreen portion of this community diminished in the north, leaving a predominantly temperate deciduous forest while the mixed temperate/evergreen community persisted in eastern Mexico.

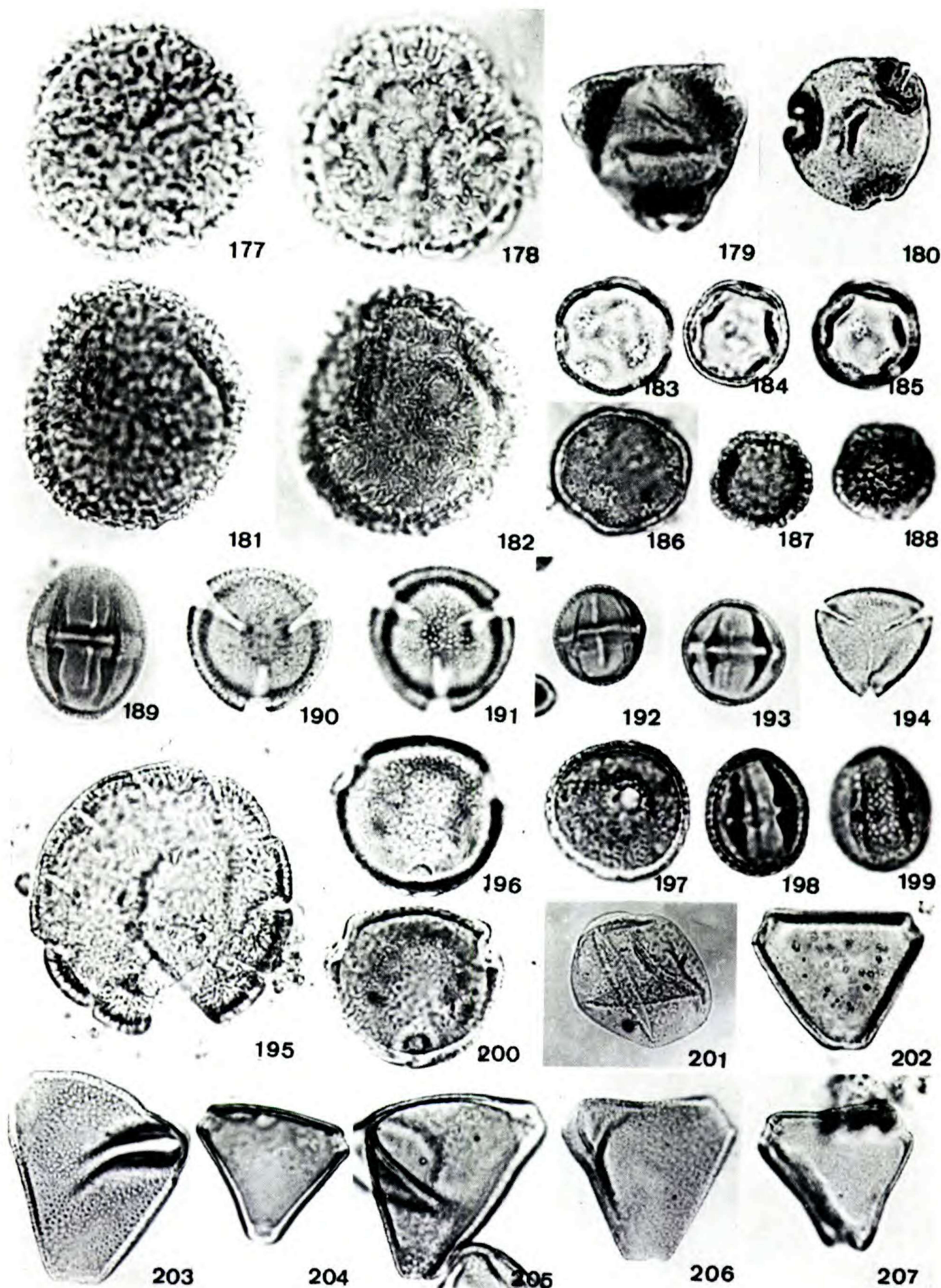
Ultimately, the model that adequately reflects the origin of floristic and faunal relationships between the eastern United States and eastern Mexico will probably provide a number of means whereby various elements of the complex could become established. As noted earlier, progressive introduction from the north is only one of several pathways available, and probably utilized by a



FIGURES 154-163.—154, 156. *Hampea/Hibiscus*.—154. 44-1, 0-23, 135 μ .—156. 45-1, U-42, 1-2, 144 μ .—155, 157. Cf. *Mezia* (?) type, 19-1, F-15,4, 74 μ .—158-159. Cf. *Malpighia*, 5-1, P-27, 36 μ .—160-161. Cf. *Hiraea*, 2-1, L-23,2, 47 μ .—162-163. *Myrica*.—162. 10-1, J-44, 36 μ .—163. 15-1, M-15, 33 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]



FIGURES 164-176.—164, 169, 174. *Ludwigia* (*Jussiaea*).—164. 30-1, J-40,2-4, 104 μ .—169. 15-1, E-36,1, 90 μ .—174. 33-1, G-28,1-3, 72 μ .—165. Cf. *Securidaca*, 13-1, L-10,1, 36 μ .—166-167. Cf. *Bredemeyera*, 13-1, E-21,3-4, 31 \times 27 μ .—168, 170-173, 175-176. *Coccoloba*.—168. 17-1, Q-42,2, 42 μ .—170-171. 30-1, K-40, 54 \times 33 μ .—172-173. 30-1, P-26,3, 58 \times 40 μ .—175-176. 32-1, X-31,2-4, 40 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]



FIGURES 177-207.—177-178, 181-182. *Passiflora*.—177-178. 19-1, X-24,4, 49 μ .—181-182. 2-1, P-38,1, 55 μ .—179-180. *Faramea*.—179. 9-1, P-33, 34 μ .—180. 13-1, G-17,1-2, 32 μ .—183-186. *Thalictrum*.—183. 13-1, Y-34,1, 26 μ .—184-185. 13-1, X-27,2-4, 24 μ .—186. 17-1, T-29,1-3, 27 μ .—187-188. *Terebrantia*, 7-1, 0-20, 22 μ .—189-193. *Rhizophora*.—189. 10-1, X-46,4, 30 \times 24 μ .—190-191. 4-1, L-18,1-2, 29 μ .—192. 51-1, R-35,2-4, 26 \times 23. μ .—193. 10-1, V-43,4, 23 μ .—194. *Eugenia/Myrcia*, 13-1, Q-30,1, 23 μ .—195. *Borreria*, 15-1, U-22,1, 59 μ .—196-197, 200. *Alibertia*.—196, 200. 15-1, L-29,2, 32 μ .—197. 33-1,

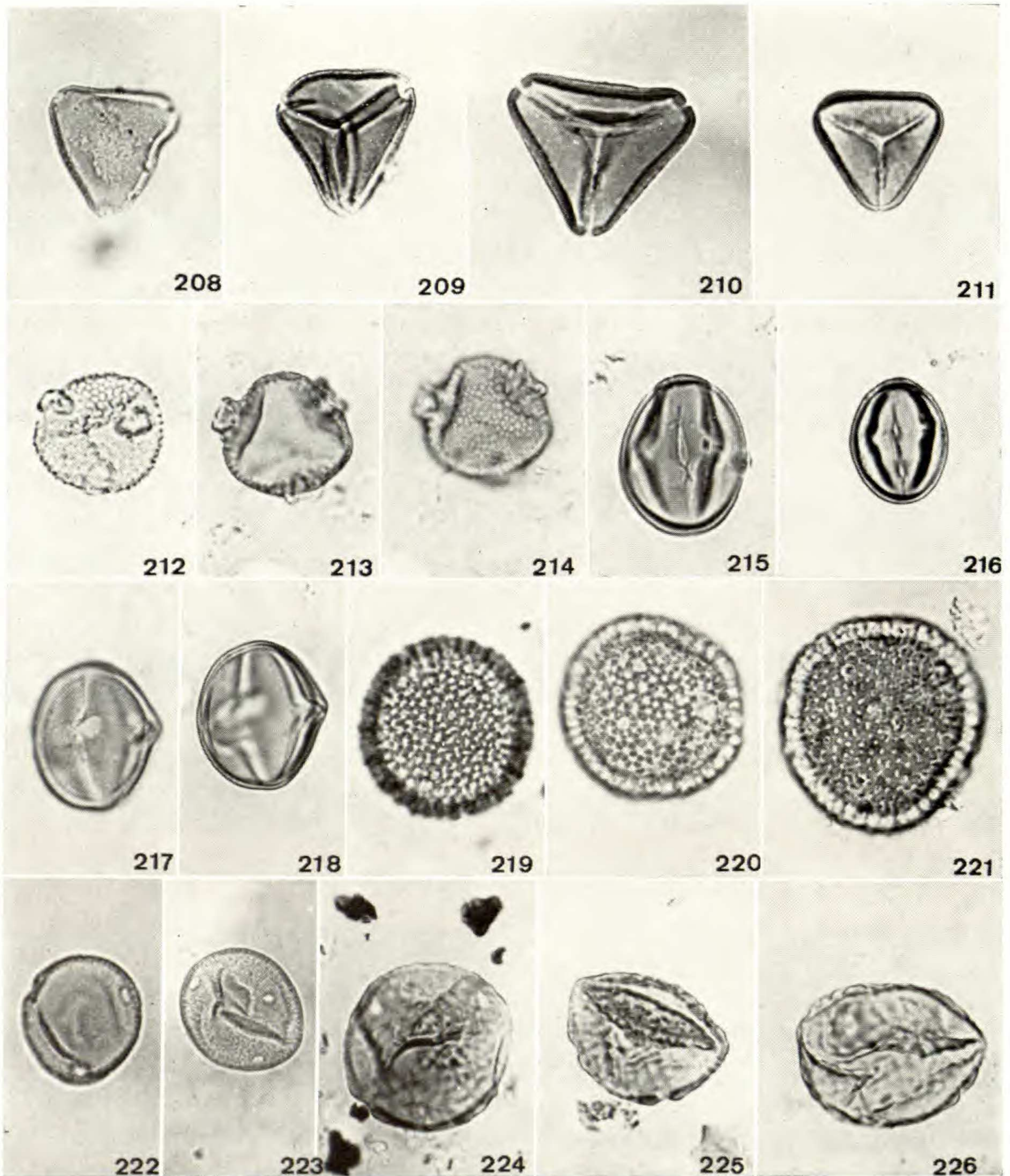
limited number of organisms. Periodic introductions throughout the Cenozoic via long-distance dispersal, and Quaternary migrations as envisioned by Deevey (1949) are also possible. Axelrod's (1975) valuable summary provides a plausible explanation for the occurrence of others. The need for further information on pre-upper Miocene Tertiary floras from southeastern Mexico is clearly evident. The meager paleobotanical data, from a single relevant study (Langenheim et al., 1967; Oligo-Miocene of Chiapas) does not record the presence of eastern United States-eastern Mexican arborescent temperate elements in Chiapas at that time.

In summary, slightly lower temperatures and greater or more uniformly distributed rainfall appears to be a logical and convenient factor in explaining the principal differences between modern and Miocene plant communities of southeastern Veracruz: the presence of *Picea*, poor representation of the High Evergreen Selva, locally extensive warm oak forests, presence of occasional temperate species in the tropical lowlands, prominent representation in lowland sediments of high altitude Needle-Leaved and mid-altitude Deciduous Forest, and the appearance of Arcto-Tertiary elements in northern Latin America corresponding in time to early phases of world-wide climatic cooling. Other consequences of lower temperatures would be increased likelihood of Paramo vegetation at the highest elevations, as previously discussed, and expanded range of the temperate grassland now preserved as relicts [*Bouteloua curtipendula* (Michx.) Torr. and *B. gracilis* (H.B.K.) Lag. ex Steud.] in the Valley of Perote.

On the basis of results from the Veracruz study, it is interesting to speculate on the history and development of the Tropical Rain Forest in Veracruz. As noted earlier, the effect of cooling climate was already evident world-wide by the end of the Miocene, continued through the Pliocene, and eventually culminated in the Pleistocene glaciations. If the rain forest was poorly developed in southeastern Veracruz in the upper Miocene because of lower temperatures, there would have been little chance for expansion and permanency during the Pliocene and Pleistocene when climates were becoming even cooler. This raises the interesting possibility that, although elements were present throughout the middle and upper Cenozoic, the High Evergreen Selva near its northern limits in Veracruz did not develop into a defined and extensive community of modern aspect and composition until post-glacial times of about 18,000–11,000 years ago (for recent discussion on dates for the end of the glacial period as evidenced in the western Gulf of Mexico, see Kennett & Shackleton, 1975). This view is in contrast with most of the older biogeographic literature which depicts the Tropical Rain Forest as an ancient assemblage occupying regions of stable, unchanging environments, and is consistent with more recent data suggesting con-

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E-34,4, 28 μ .—198–199. *Meliosma*, 40-1, U-34,3, 27 \times 23 μ .—201. *Populus*, 2-1, B-27, 36 μ .—202–203. *Paullinia*.—202. 8-1, V-49,3-4, 35 μ .—203. 10-1, G-26,4, 36 μ .—204–207. *Serjania*. 204. 25-1, L-38,2-4, 27 μ .—205. 4-1, U-16,1, 36 μ .—206. 49-1, Q-43,1, 40 μ .—207. 13-1, J-25,2, 35 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]



FIGURES 208-226.—208. *Allophylus*, 10-1, N-24,3, 25 μ .—209. *Cupania*, 2-1, G-22,1, 28 μ .—210-211. *Matayba*.—210. 2-1, N-44,3, 31 μ .—211. 25-1, N-12, 22 μ .—212-214. *Buettneria*.—212. 13-1, W-43, 23 μ .—213-214. 37-1, F-25, 27 μ .—215-218. *Cleyera*.—215. 17-1, T-11, 32 \times 24 μ .—216. 33-1, J-48,2, 27 μ .—217-218. 17-1, U-25, 28 \times 24 μ .—219-221. *Daphnopsis*.—219. 17-1, P-11, 36 μ .—220. 25-1, T-39,3, 42 μ .—221. 17-1, H-12,2, 40 μ .—222-223. *Celtis*.—222. 17-1, U-45, 32 μ .—223. 2-1, C-50,1, 35 μ .—224-226. *Ulmus*.—224. 38-1, M-33,3, 36 μ .—225. 33-1, N-48,1-2, 31 μ .—226. 37-1, M-13,1, 34 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

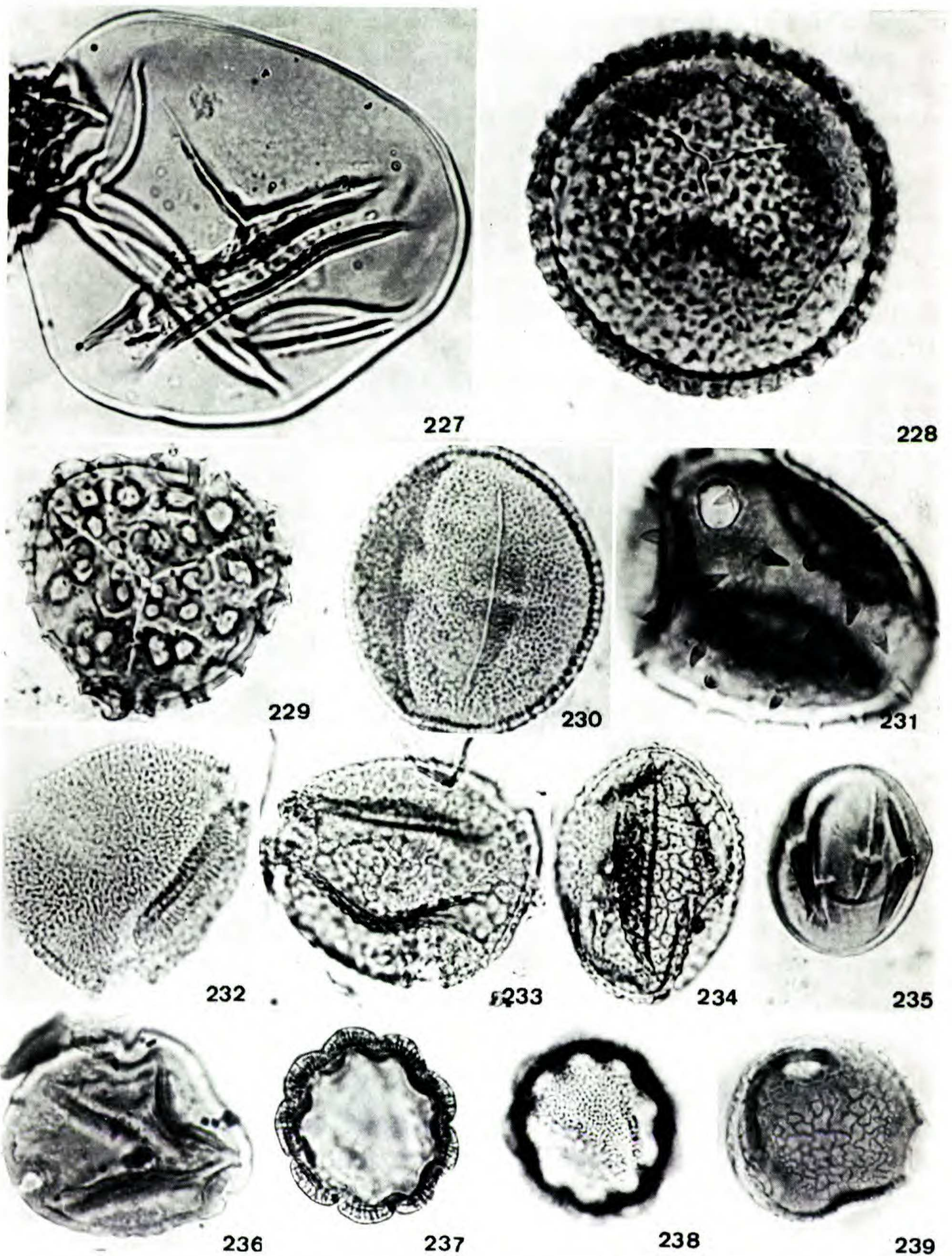
siderable alteration in range and composition of the rain forest during the last few million years (Haffer, 1969, 1970, 1974; Vanzolini, 1973; Vanzolini & Williams, 1970; Vuilleumier, 1971). The relevancy of this new concept of rain forest history to speciation models is briefly discussed by Graham (1975).

Regarding moisture regimes during the upper Miocene, there is some evidence for slightly increased rainfall or more uniform distribution with no pronounced dry season. Sousa (pers. comm., 1973) believes fossil pollen of *Picea* in Veracruz implies more moisture as well as cooler climates. This view is supported by the absence of desert vegetation and only minor representation of the Low Evergreen Selva, Low Thorn Selva, and Thorn Scrub. The presence of *Cupania*, *Celtis*, *Casearia*, *Daphnopsis*, *Eugenia*, *Ilex*, cf. *Acacia*, *Bursera*, cf. *Sapium*, *Comocladia*, cf. *Brahea*, and *Combretum* (Fig. 5) may reflect a modified Low Deciduous Selva occupying restricted areas of edaphically or physiographically induced moisture stress. These ecotypes are important in the dynamics of vegetational history since in more recent times they have coalesced with other pre-adapted subhumid elements to form the modern xeric communities of Veracruz. In the upper Miocene, however, they were not, as a community, a conspicuous or widespread component of the vegetation.

The last category of communities apparently absent from the upper Miocene landscape are those suspected of resulting from human activity. The natural origin and antiquity of the Low Semi-Evergreen Selva, Savannas, and Palm Stands (especially *Scheelea* and *Sabal*) in Veracruz have never been satisfactorily resolved. The prevalent view is that the present extent, if not the origin, of these associations resulted from agricultural practices of sedentary populations (milpa farming). These studies are relevant only in demonstrating that the Low Semi-Evergreen Selva, Savannas, and Palm Stands were not prominent members of the natural vegetation, and are at least of post-Miocene development.

The evolution of plant communities in southeastern Veracruz since the upper Miocene has involved three principal changes in the flora. Elements of the High Evergreen Selva have coalesced into the dominant natural community of the modern southern Veracruz lowlands, with concomitant elimination of *Picea* from Veracruz and elsewhere in southern Mexico (Ohngemach, unpublished data). This is likely due to increasing minimum temperatures, in contrast to those of the upper Miocene, and perhaps occurred as late as 18,000–11,000 B. P. (Kennett & Shackleton, 1975). Elements preadapted to arid environments expanded and coalesced into communities as a result of a slight decrease or redistribution of rainfall, but facilitated by the rise of the Sierra de Los Tuxtlas and more recently by human modification of the environment. The last stage in the evolution of the Veracruz flora has been the appearance of Low Semi-Evergreen Selvas, Savannas, and Palm Stands resulting more directly from human activity.

A complete statement on the Cenozoic history of vegetation in southeastern Veracruz will require further paleobotanical studies of progressively younger floras. Of particular importance will be pollen analytical studies of Pleistocene sediments. Two events during that epoch may prove to be critical in understanding certain features of the Veracruz flora. The Hypsithermal Interval (xerothermic period, pine maximum) is a debated aspect of Quaternary paleo-



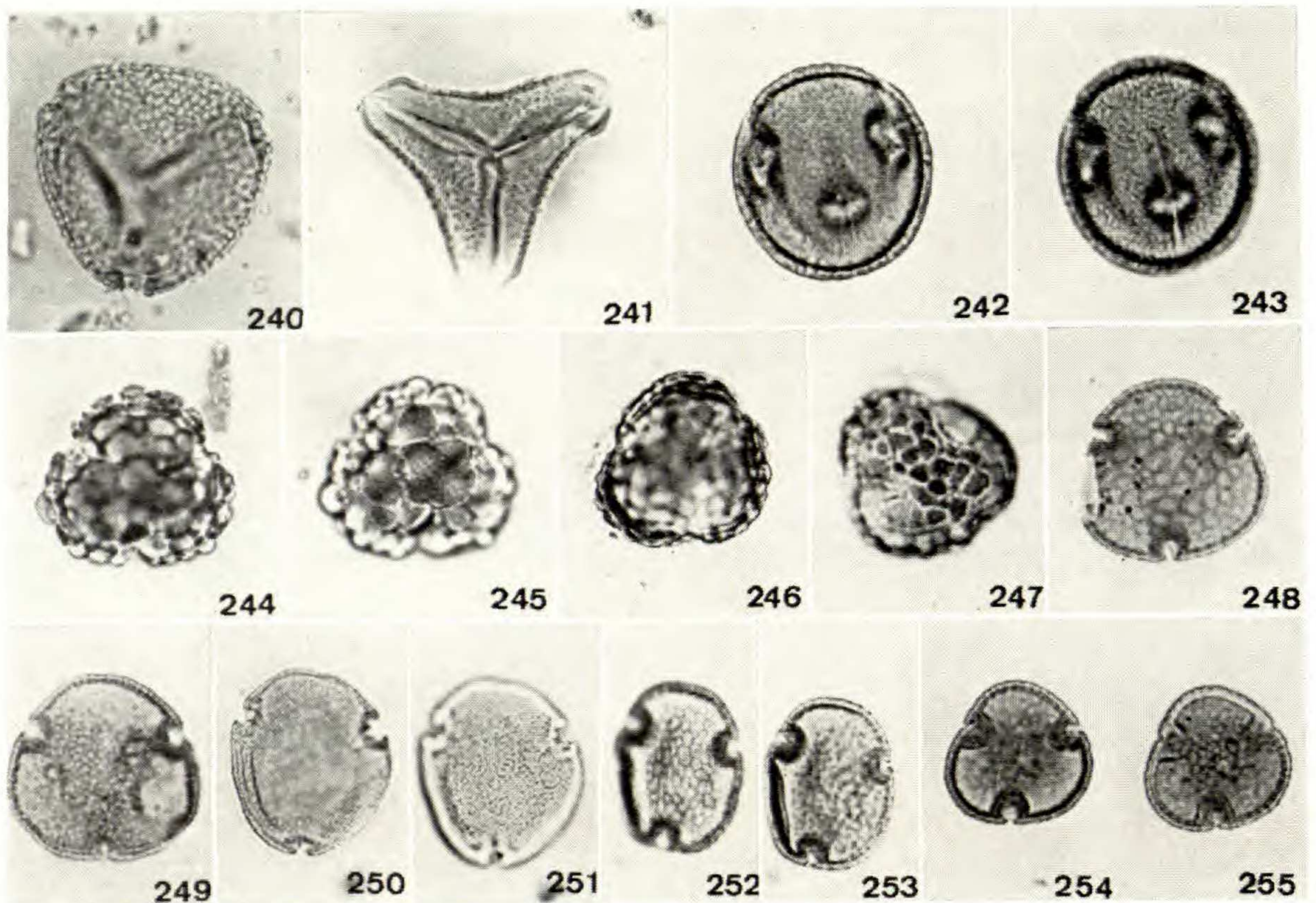
FIGURES 227-239. Selected unknowns from the Paraje Solo microflora.—227. 4-1, A-35, 2-4, 90 μ .—228. 30-1, B-23,1, 80 μ .—229. 10-1, C-45, 65 μ .—230-231. Cf. Cucurbitaceae.—230. 37-1, B-30,1-2, 65 \times 55 μ .—231. 10-1, C-32,3, 75 μ .—232. Cf. Apocynaceae, e.g., *Thevelia*. 49-1, R-44,3, 55 μ .—233-234. Cf. *Mucuna*?—233. 15-1, T-37, 58 μ .—234. 13-1, C-37,4, 60 \times 45 μ .—235. Cf. Flacourtiaceae, e.g., *Zuelania*. 38-1, C-37, 40 \times 35 μ .—236. 4-1, S-22,1, 45 μ .—237-238. Cf. Rubiaceae, 13-1, G-24, 44 μ .—239. 4-1, K-49, 49 μ . [The numbers following plant names represent sample and slide number, England Slide Finder coordinates, and size.]

ecology, especially in tropical regions. Broadly defined it is a period of about 4,000 years duration, between 8,000 to 4,000 B. P., during which climates were warmer and drier than at present. The closing date for the interval is of interest because Coe (pers. comm., 1973) and his associates have found evidence of a sedentary population in southern Veracruz dating from about 2,900 B. C. (ca. 4,900 B. P.). The Veracruz lowlands and adjacent regions are classically referred to as the "Olmec Heartland" and contains some of the earliest evidence of sedentary habitation in northern Latin America. Studies by Coe at San Lorenzo have shown that "pottery-using, sedentary, corn-growing peoples were in the area by 1,500 B. C. Three centuries later (ca. 1,200 B. C.) the archeological Olmec culture appears fully developed at San Lorenzo" (Coe, pers. comm., 1973). The earlier date of 2,900 B. C. is from a preceramic culture named by Jeffrey Wilkerson as Palo Hueco, at a site called Santa Luisa in the Tecolotea drainage. It is interesting to speculate on the consequences of an expanding farming population developing near the culmination of a climatically dry period. One effect may have been to accelerate the development and expand the range of Savannas, the Low Semi-Evergreen Selva, and Palm Stands. Evidence of a post-glacial dry period, anthropogenic modification of natural vegetation, and time of appearance of arid communities of plants would be significant contributions resulting from Quaternary pollen studies in southern Veracruz.

CONCLUSIONS

The upper Miocene paleocommunities of south coastal Veracruz show similarities and some distinct differences from present-day plant associations. Among communities well represented in the Paraje Solo assemblage are the Needle-Leaved Forests of Bosque de Oyamel (including *Picea* now restricted to the highlands of northern Mexico), Bosque de Pino, and Bosque de Pino y Encino; a lowland warm oak, and possibly upland temperate and evergreen Broad-Leaved Forest; Bosque Caducifolio (oak-*Liquidambar* Deciduous Forest); Saline and possibly Temperate Grasslands; Mangrove Swamps; Coastal Dune Vegetation; and vegetation occupying restricted areas of physiographically or edaphically controlled moisture deficits comparable to a modified Low Deciduous Selva. Other communities likely present were the Paramo, Inland Swamps, and Aquatic Vegetation, even though for reasons discussed, pollen of the dominants are absent or poorly represented in the microflora.

Other vegetation types forming an important part of the modern flora were not major components of the upper Miocene vegetation. These include the High Evergreen Selva, High Semi-Evergreen Selva, Medium Semi-Evergreen Selva, Low Evergreen Selva, Low Semi-Evergreen Selva, and communities of more arid aspect as the Scale-Leaved Forest, Low Thorn Selva, *Nolina-Hechtia-Agave* Desert, and Thorn Scrub. Two communities possibly resulting from ancient agricultural practices in the "Olmec Heartland" (Palm Stands and Savannas) were also poorly represented in the microflora. A change in two environmental factors simultaneously explains both the wide-spread occurrence of temperate communities and the restricted distribution of tropical and arid vegetation. It is



FIGURES 240–255. Selected unknowns from the Paraje Solo microflora.—240. 32-1, W-16,3, 36 μ .—241. Loranthaceae, 2-1, D-12,1-3, 42 μ .—242–243. Cf. Flacourtiaceae, e.g., *Laetia*, 35-1, R-18,2, 32 μ .—244–245. Cf. *Calamus*, Palmae, Old World; cf. one grain of a polyad of *Dichrostachys*, Leguminosae, Old World, 2-1, C-40,2-4, 40 μ .—246–247. Cf. Haloragidaceae, e.g., *Proserpinaca*, 8-1, T-25, 27 μ .—248–255. Cf. Sterculiaceae.—248. 34-1, Q-46,4, 27 μ .—249. 34-1, L-30,1-3, 27 μ .—250–251. 10-1, J-14,1, 30 μ .—252–253. 8-1, U-36,2, 25 μ .—254–255. 25-1, U-41,2-4, 23 μ . [The numbers following plant names represent sample and number, England Slide Finder coordinates, and size.]

likely that climates in southeastern Mexico during the upper Miocene were cooler (e.g., more temperate and seasonal), and with possibly increased or more uniformly distributed rainfall than in the present warm inter-glacial environments.

In discussing the upper Miocene character of Veracruz communities it is not assumed that all members of the Tropical Rain Forest or vegetation of drier aspect were absent from the region. Vegetational history studies have progressed beyond the point of expecting paleocommunities, especially in areas of significant physiographic relief, to rigidly conform in composition to static geoflora-type assemblages. Elements representing a variety of ecotypes are easily accommodated in the topographically diverse region of southern Veracruz. The manner in which these various elements coalesce to form communities, the composition of these communities, and the areal extent they occupy depends on the existing set of environmental conditions and the vicissitudes of seed availability. Within pollen transport range of the Paraje Solo depositional environment, temperate communities during the upper Miocene were well developed in comparison to the tropical and more arid vegetation that presently characterizes the area.

Similarly, the paleoenvironments reconstructed to account for these differences between fossil and modern vegetation involve a complex mosaic of inter-related factors. In addition to a cooler, more seasonal climate it is likely that the higher sea levels of upper Miocene time, prior to the wide-spread development of continental ice sheets, inundated portions of the Veracruz lowland and physically reduced the area available to rain forest development.

These considerations emphasize the dynamic aspect of vegetation and are important concepts in understanding the geologic evolution of communities. Of particular interest is the recent change in view concerning the "stability" of the Tropical Rain Forest. Considering the lowland habitat of sizable portions of the Neotropical rain forest, with its susceptibility to changes in sea level, it may be that this community is actually a delicately balanced ephemeral assemblage that has undergone greater changes in range and composition during the later Cenozoic than more northern temperate biotas closer to the glacial boundary.

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